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Cover photo: Female *Gambequezonia itimana* (Salticidae) from Los Banos, Luzon Island, Phillippines. Photo by Robert Jackson.

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First record of the trapdoor spider genus *Conothele* (Araneae, Ctenizidae) from India, with a description of two new species

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Abstract. The genus *Conothele* of the trapdoor family Ctenizidae is reported for the first time from India with the description of two new species *Conothele varvarti* from Similipal Tiger Reserve in Orissa, eastern India and *C. vali* from Tawang district in Arunachal Pradesh, northeastern India. The genus was previously considered arboreal in habit but the present record reveals that these two species are strictly ground dwelling. Notes on the natural history are provided for both species.

Keywords: Arunachal Pradesh, new species, Orissa, ground dwelling, arboreal

The family Ctenizidae (Orthognatha, Mygalomorphae) is one of the four families of trapdoor spiders found in India (Siliwal & Molur 2007). This family is represented by nine genera and 121 species from around the world (Platnick 2008). Only one genus *Latouchia* Pocock 1901 and one species *L. cryptica* (Simon 1897) is formally reported from India. Although, Gravely (1915, 1935) in his publications on Indian mygalomorph spiders included the genus *Conothele* Thorell 1878 based on a few unidentified specimens in the Indian Museum (now Zoological Survey of India), the genus was never formally described nor any species listed from India.

The genus *Conothele* was erected by Thorell in 1878 to accommodate *Conothele malayana* (Doleschall 1859), which was originally misplaced in the genus *Cteniza* Latreille 1829. Since then many new species of *Conothele* have been described (Thorell 1881, 1887, 1890; Pocock 1898, 1899; Kulczyn'ski 1908; Strand 1913; Hogg 1914; Chamberlin 1917; Berland 1938; Saaristo 2002; Platnick 2008). In his revision of the infraorder Mygalomorphae, Raven (1985) synonymized the genus *Lechrictenus* Chamberlin 1917 with *Conothele*. Some species of *Ummidia* Thorell 1875 were transferred to *Conothele* (Raven 1985; Haupt 2006). The genus *Conothele* is known from 16 species and has a wide distribution range extending from Myanmar to Australia (Platnick 2008).

In this paper, two new species of *Conothele* are deseribed based on female specimens collected from Orissa and Arunachal Pradesh. Males of the species could not be found even after repeated searching in the area where females were collected. Considering the significance of this find, we formally report the occurrence of the genus *Conothele* from India. It also confirms the earlier reports by Gravely (1915, 1935) of the existence of this genus in India. Information on the habitat, behavior, and burrow of the two new species are provided. Interestingly, in the present study, these spiders were found strictly ground dwelling though previously the genus was considered arboreal in habit (Pocock 1900; Gravely 1935). We provide information on the burrow structure of these spiders, which is unique in comparison with other members of this genus.

The two new species from India are considered different from the rest of the known species of *Conothele* described from various islands of Australasia because of the geographical distribution. Geographically, the species closest in distribution to this new species is *Conothele birmanica* Thorell 1887 from Myanmar. RR examined the type specimen of *C. birmanica* at The Natural History Museum, London but spermathecae was not dissected, hence the information is lacking in this paper. Comparison with *C. birmanica* and *C. taiwanensis* Tso et al. 2003 is based only on available literature (Pocock 1900; Tso et al. 2003).

METHODS

Spiders were collected during the theraphosid spider surveys conducted in the year 2005 and 2007 in Arunachal Pradesh and Orissa respectively. The specimens are deposited at Wildlife Information Liaison Development Society, Coimbatore, Tamil Nadu. Measurements of body parts except for the eyes were taken with a MitutoyoTM Vernier Caliper. Eye measurements were done with a calibrated ocular micrometer. All measurements are in mm. Spermathecae were dissected and cleaned in concentrated laetic acid in 100°C water bath for 15–20 minutes. All illustrations were prepared with the help of camera lueida attached to a CETII™ stereomicroscope by MS.

Abbreviations: ALE = anterior lateral eye, AME = anterior median eye, MOQ = median ocular quadrate, PLE = posterior lateral eye, PME = posterior median eye, PLS = posterior later spinnerets, PMS = posterior median spinnerets, WILD = Wildlife Information Liaison Development Society. Abbreviations used for hair and spines count are d = dorsal, fe = femur, mt = metatarsus, p = prolateral, pa = patella, r = retrolateral, ta = tarsus, ti = tibia, v = ventral.

TAXONOMY

Conothele Thorell 1878

Conothele Thorell 1878:303; Simon 1892:88; Pocock 1900:165

Type.—*Conothele malayana* (Doleschall 1859) designated based on a female specimen. Not examined.

Diagnosis.—It differs from other known genera of this family by trochanters I and II ventrally not notched (Raven 1985); tibia III consists of saddle-shape depression on the basal upper part (Figs. 8, 23) as seen in *Ummidia* (Pocock 1900; Raven 1985).

Conothele varvarti new species
(Figs. 1–15)

Type specimens.—INDIA: *Orissa*: holotype female, Barehipani road, Chahala range, Similipal Tiger Reserve, 744 m elev., 21°57′46.2″ N, 86°20′23.4″E, 31 March 2007, Manoj V. Nair (WILD-07-ARA-163); *Orissa*, 1 paratype female, Ramthirtha, Jashipur, 419 m elev., 21°57′08.4″N, 86°04′14.0″E, 29 August 2007, M. Siliwal (WILD-07-ARA-207).

Other material examined.—INDIA: *Orissa*: 1 subadult ♀, Barehipani road, Chahala range, Similipal Tiger Reserve, 744 m elev., 21°57′46.2″N, 86°20′23.4″E, 31 March 2007, M. Nair (WILD-07-ARA-164); 2 immatures, Baniabasa, Udala range, Similipal Tiger Reserve, 545 m elev., 21°44′03.2″N, 86°26′51.8″E, 27 April 2007, Manoj V. Nair (WILD-07-ARA-165, 166); 2 immatures, before check gate of Jacum range, periphery of Karlapat Wildlife Sanctuary, 336 m elev., 19°44′49.3″N, 83°06′27.4″E, 14 April 2007, M. Siliwal, S. Behera (WILD-07-ARA-167, 168).

Diagnosis.—It differs from other known species of this genus by the posterior row of eyes weakly procurved (Fig. 3), (PRE straight in *C. birmanica*; PRE recurved *C. taiwanensis*); abdomen dorsally warty/rough (Fig. 1); spermathecae with bowl-shaped apical lobe on a stalk, which is twisted twice distally (Fig. 12) and carapace slightly shorter than patella and tibia of leg I and IV. It differs from *C. birmanica* by curved spines on tibiae I–II (Fig. 7).

Etymology.—The name of the species is based on the Sanskrit root of the word wart, referring to the warty appearance of the spider's abdomen.

Description of female holotype.—Total length, 15.52; carapace 5.52 long, 5.1 wide; chelicerae 2.42 intact. Abdomen 10.0 long, 6.84 wide. Spinnerets: PMS, 0.9 long, 0.3 wide, 0.1 apart; PLS, 2.0 total length (1.2 basal, 0.5 middle, 0.3 distal; mid-widths 1.1, 0.8, 0.65 respectively). Morphometry of legs and palp is given in Table 1.

Carapace: reddish-brown, glabrous except for five long hairs on caput, few lines of depression along interstitial ridges (Figs. 1, 2), weak crenulations on caput, more conspicuous near eye group and anteriolaterally, elsewhere absent or inconspicuous. Caput with distinct mound between fovea and eyes (Fig. 2). Fovea deep, procurved, U-shaped (Fig. 1).

Eyes (Fig. 3)*:* eight in two rows, both rows procurved, posterior row slightly procurved, ocular group 0.8 long, 1.2 wide, about 0.3 of headwidth; diameter AME 0.3, PME 0.15, ALE 0.4, PLE 0.25; distance between ALE–AME 0.1, AME–AME 0.05, PLE–PME adjacent, PME–PME 0.4, ALE–ALE 0.6, ALE–PLE 0.2; MOQ not square, 0.6 long, 0.6 front width, 0.7 back width; clypeus 0.6 high.

Maxillae (Fig. 4)*:* 1.7 long in front, 2.5 long in back, 1.4 wide; cuspule numbers not same on right and left maxillae, right maxillae with 14 small cuspules on prolateral-proximal corner, 16 large ones ventrally in ¾ of length, left maxillae with 8 small cuspules on prolateral-proximal corner, 17 large ventrally in ¾ of length. Anterior lobe absent or greatly reduced.

Labium (Fig. 4)*:* 1.0 long, 1.4 wide, labiosternal groove shallow and slightly concave, 5 large cuspules in three rows (2 + 2 + 1) centrally, size of cuspules similar to that on maxillae.

Chelicerae (Fig. 5)*:* 4 large promarginal teeth, 5 large and 1 very small retromarginal teeth, basomesal teeth absent; rastellum conspicuous, raised on a low mound, consisting of 12 thick spines on vertical face and up, of which 10 are in anterior row; many long and short spines present along anterior dorsal surface.

Sternum (Fig. 4)*:* broader posteriorly, reddish-brown, with elevated anterior and lateral sides, sloping posteriorly, 3.68 long, 3.2 wide, covered with long black hair, more dense towards lateral sides, posterior angle blunt and not separating coxae IV. Sigilla large, irregular shape, centrally placed. Non-sigillate area with fine corrugations.

Legs: all legs similar in thickness, reddish-brown above and light yellowish-brown below except tarsi of palp and metatarsi and tarsi of all legs that are black above and reddish-brown below. Tibiae, metatarsi and tarsi of leg I–II and tibiae and tarsi of palp dorsoventrally flattened. Femora III clearly wider than rest. Tibiae III with saddle-shaped depression on basal upper part. Metatarsi of leg I, II, IV longer than tarsi. Metatarsal preening combs absent on all legs. Coxae of legs reddish-brown ventrally. Legs covered with sparsely distributed hair, bristles, and few curved thick thorn-like spines (Figs. 6–8). Two conspicuous hairless bands running over length of femora, patellae, and tibiae. Scopulae and claw tufts absent on tarsi of all legs and palp (Figs. 6–8). Leg formula 4132.

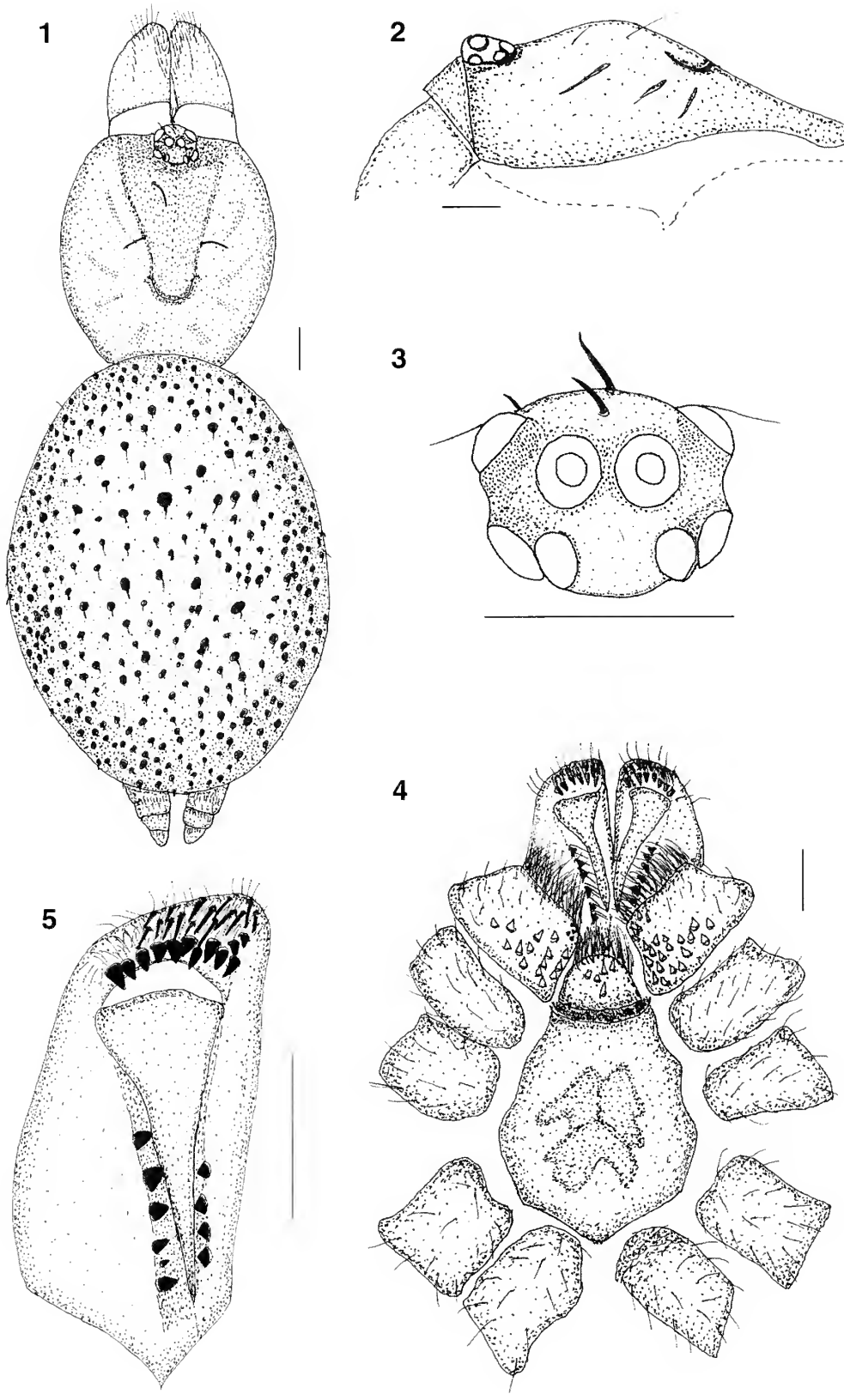
Spines (Figs. 6–8)*:* curved thick thorn-like spines, ti I, p = 38, r = 41; mt I, p = 34, r = 24; ta I, p = 26, r = 15; ti II, p = 26, r = 21; mt II, p = 30, r = 8; ta II, p = 23, r = 7; pa III, p = 10; ti III, p = 3; mt III, d = 4; ta III, p = 9, r = 3; mt IV, p = 3; ta IV, p = 6; palp, pa, p = 1; ti, p = 46 + 2 broken, r = 41; ta, p = 45+2 broken, r = 43.

Trichobothria: mt I–II with 10 filiform trichobothria in two rows in distal half; ta I with 4 clavate trichobothria centrally, 12 filiform in two longitudinal rows; ta II with 7 clavate in basal one fourth, 10 filiform in two longitudinal rows; ta III with 4 clavate in basal one fourth, 16 filiform in two longitudinal rows; ta IV with 2 clavate basal, 5 filiform in two rows in distal half; palp, ti with 10–12 filiform in two curved rows; ta with 5 clavate in center, 12 filiform in 2 longitudinal rows.

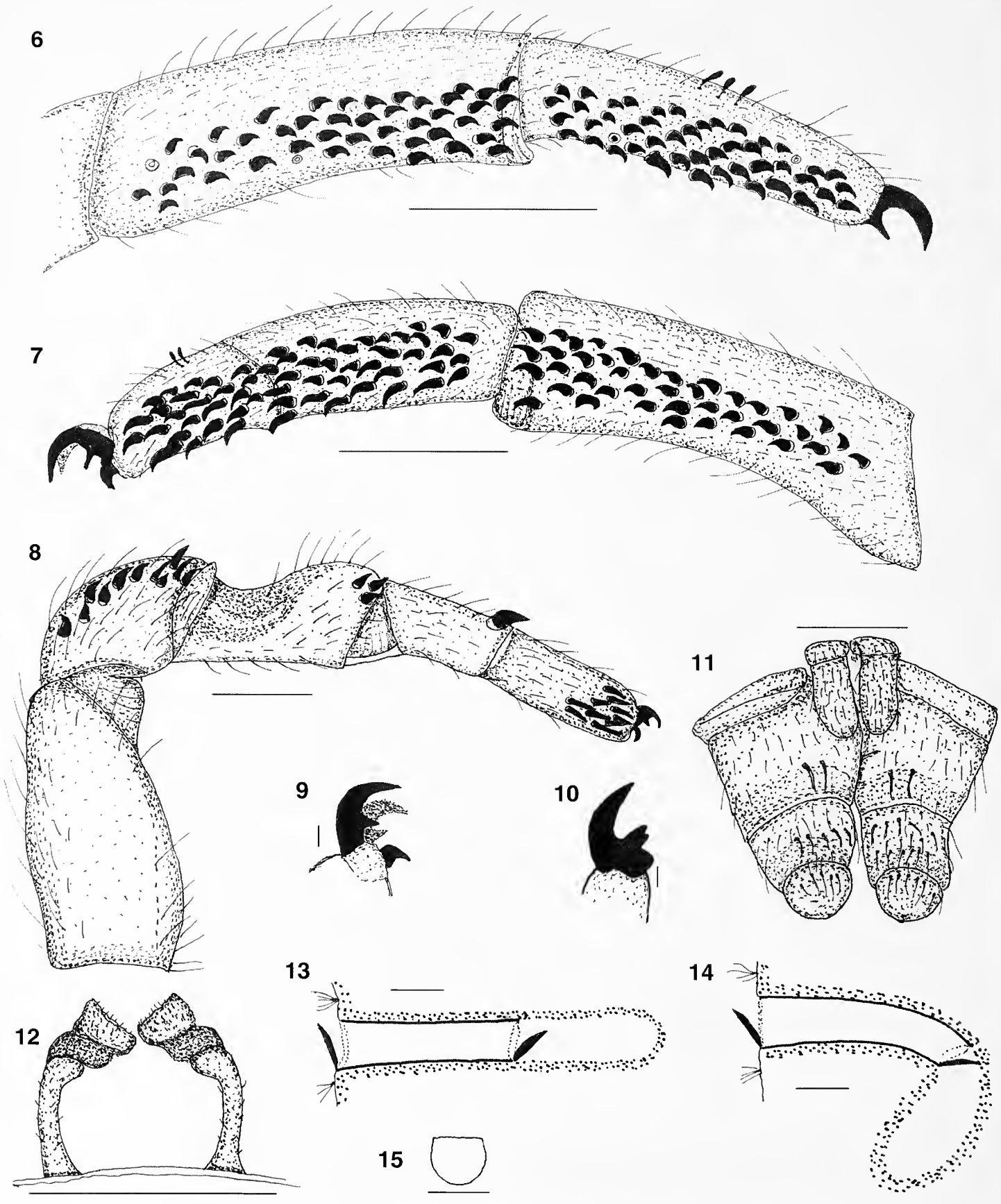
Leg coxae: coxa IV slightly wider than III, I and II subequal.

Claws: all legs with three claws, paired claw with single tooth (Fig. 9). Palp with single claw bearing a single unequal bifid tooth (Fig. 10).

Abdomen: grayish-brown, with few yellow small spots, covered with short and long thorn-like setae and several bristles, which gives it a warty appearance (Fig. 1); one in 6–8 thorns is long and is about 2–3 times longer and slightly



Figures 1–5.—*Conothele varvarti* new species, female: 1. Cephalothorax and abdomen, dorsal view; 2. Cephalothorax, lateral view; 3. Eyes; 4. Sternum, labium, maxillae and chelicerae; 5. Chelicerae, rastellum, promarginal and retromarginal teeth. Scale = 1.0 mm.



Figures 6–15.—*Conothele varvarti* new species, female: 6. Tibia and tarsus of palp, prolateral view; 7. Tibia, metatarsus and tarsus of leg I, prloateral view; 8. Leg III (femur to tarsus) prolateral view; 9. Claw of leg I; 10. Claw of palp; 11. Spinnerets; 12. Spermathecae; 13, 14. Burrow structure; 15. Hinged door. Scale = 1.0 mm (Figs. 6–8, 11, 12); 0.1 mm (Figs. 9, 10); 10.0 mm (Figs. 13–15).

Table 1.—Morphometry of legs and palp of the holotype female (WILD-07-ARA-163) and paratype female (WILD-07-ARA-207) of *Conothele varvarti* new species.

	Leg I		Leg II		Leg III		Leg IV		Palp	
	Holo #163	Para #207	Holo #163	Para #207	Holo #163	Para #207	Holo #163	Para #207	Holo #163	Para #207
Femur	4.2	2.84	3.30	2.44	3.12	2.24	4.0	3.12	4.24	3.34
Patella	2.46	2.10	2.14	1.66	2.0	1.56	2.36	2.14	2.16	1.44
Tibia	3.12	2.18	1.9	1.42	1.74	1.78	2.92	2.3	3.0	1.7
Metatarsus	1.42	1.12	1.46	1.10	1.26	1.0	2.42	1.86	-	-
Tarsus	1.32	0.9	1.12	0.9	1.96	1.44	1.72	0.88	2.3	1.8
Total	12.52	9.14	9.92	7.52	10.08	8.02	13.42	10.3	11.7	8.28
					Midwidth					
Femur	1.0	0.64	0.9	0.52	1.42	0.94	1.2	0.64	1.1	0.62
Tibia	1.06	0.72	0.96	0.68	1.0	0.72	1.0	0.72	1.0	0.72

thicker than short thorns. Ventrally yellowish, faint black patch above book lungs, uniformly covered with short and long bristles.

Spinnerets: PMS digitiform covered with brown hair; PLS, covered with brown hair, apical segment dome-shape (Fig. 11).

Spermathecae: bowl-shape apical lobe on a stalk, which is twisted twice distally (Fig. 12).

Description of female paratype (WILD-07-ARA-204).—Total length 11.24; carapace 4.52 long 3.44 wide; chelicerae 1.36 long intact, 8 retromarginal and 4 promarginal teeth. Sternum 2.24 long, 2.0 wide. Labium 0.64 long, 0.96.2 wide, 9 large cuspules in 3 rows (5 + 2 + 2). Maxillae 2.06 long back, 1.28 long front, 1.08 wide, cuspules 20–24 of varying size in angular shape. Abdomen 6.72 long and 5.18 wide. Spinnerets: PMS, 0.6 long, 0.2 wide, 0.14 apart; PLS, 1.44 total length (0.72 basal, 0.42 middle, 0.3 distal; midwidths 0.8, 0.56, 0.34 respectively). Morphometry of leg and palp given in Table 1. Rest of the characters are same as holotype (WILD-07-ARA-163).

Distribution.—India, Orissa: Chahala, Upper Barahkamura, Jenabil and Baniabasa ranges in Similipal Tiger Reserve, Maurbhanj district; Ramthirtha in Jashipur; Karlapat Wildlife Sanctuary in Kalahandi district.

NATURAL HISTORY

Individuals of *C. varvarti* new species were found throughout Similipal Tiger Reserve, where more than 30 burrows of various sizes were located and almost all were found on mossy roadside cuttings close to the ground and up to 1.5 m, both in open and closed canopy areas. Similarly, several burrows of the species were located on roadside bunds in the periphery of Karlapat WLS in southern Orissa suggesting the species to be ground dwelling. This differs from what was previously reported by Pocock (1900) that the spiders of this genus from Myanmar and islands of Australasia were arboreal in habit with their trapdoor retreats on tree trunks. Also, Gravely (1935) reported a male of this genus in a retreat built in deodar *Cedrus deodara* humus, which he mentions as unusual since these spider retreats were generally found on tree trunks.

The burrow of *C. varvarti* new species consists of a short silken tube about 60–70 mm long and 15–22 mm wide, and mostly aligned perpendicular to the angle of the slope of roadside bund (Figs. 13,14). The entrance of the burrow is closed with a moderately thick D-shaped hinged trapdoor (about 15 mm wide), with the attached side being straight rather than curved (Fig. 15). Also, the door hinge is mostly at the base or on the sides of the entrance but never at the top. The trapdoor is well camouflaged with soil and bits of dried leaves and moss. On the inner end of the burrow a second D-shaped hinged trapdoor exists, which opens into another chamber or retreat devoid of any silk lining (Figs. 13, 14). This unique burrow structure is probably a strategy to escape from intruders.

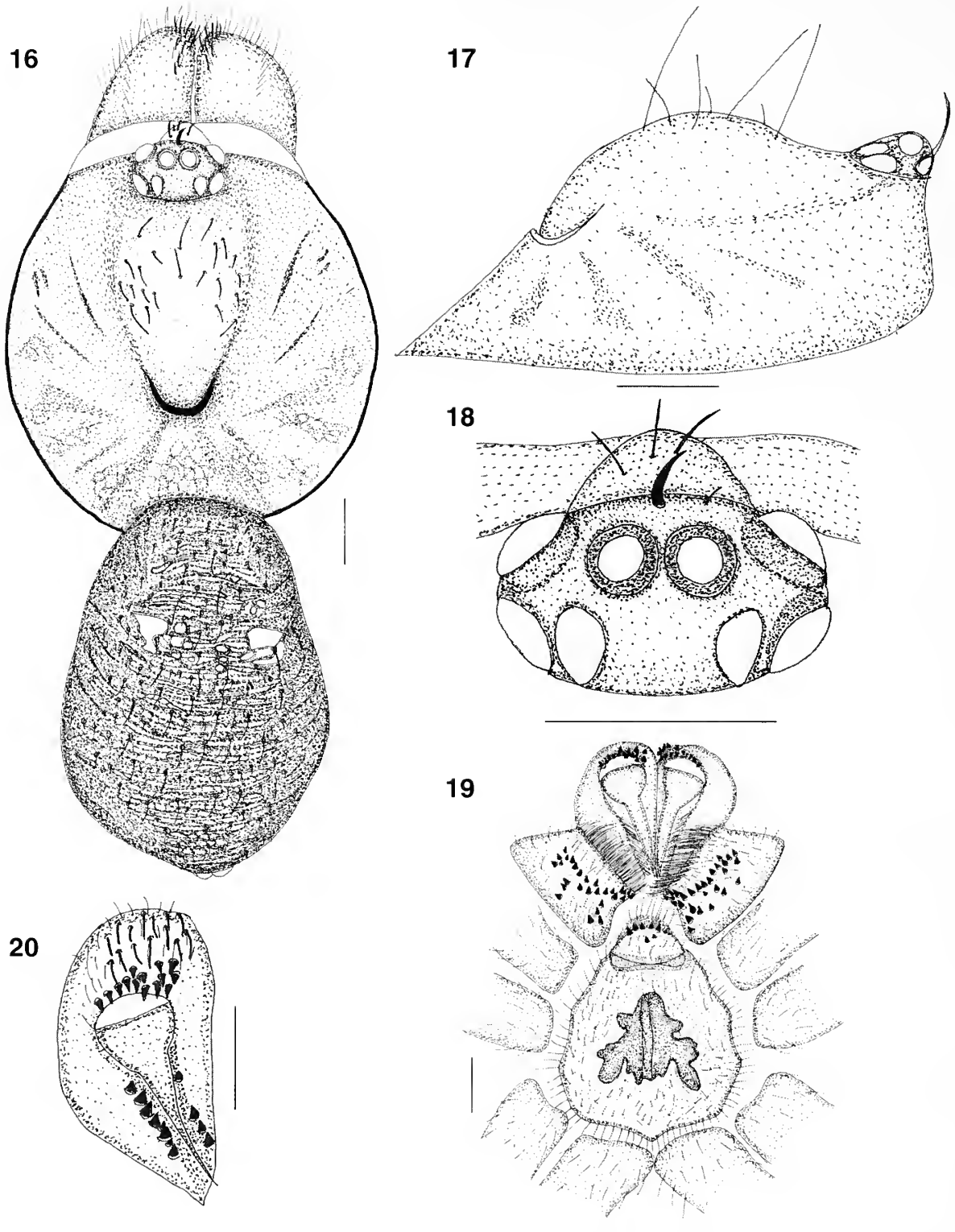
Conothele vali new species
(Figs. 16–27)

Type specimen.—INDIA: *Arunachal Pradesh*: holotype female, near Shurbi village, Tawang District, 1856 m elev., 27°33′27.2″N, 91°53′41.5″E, 13 May 2005, M. Siliwal (WILD-05-ARA-77).

Diagnosis.—It differs from other known species of this genus in having posterior row of eyes weakly procurved (Fig. 18) as seen in *C. varvarti* new species (PRE straight in *C. birmanica*; PRE recurved *C. taiwanensis*); eight cuspules on labium (Fig. 19) (5 cuspules of *C. brimanica* and *C. varvarti* new species; 14 cuspules in *C. taiwanensis*); 3 small and 26–28 large cuspules on maxillae (Fig. 19) (8 small and 16–17 large cuspules in *C. varvarti*; 53 cuspules in *C. taiwanensis*); abdomen heavily wrinkled (Fig. 16) (warty in *C. varvarti*, normal in *C. birmanica* and *C. taiwanensis*); spermathecae with globular apical lobe on a stalk, which is bent twice distally in zigzag manner (Fig. 27) (in *C. varvarti*, stalk is twisted twice and anterior lobe is bowl- shape; stalk right-angled curve at apical globe in *C. taiwanensis*); it differs from *C. brimanica* by curved spines on tibiae I–II (Figs. 21, 22); it differs from *C. varvarti* in leg formula 4123 (4132 in *C. varvarti*, Table 2); paired claws on all the legs with two unequal teeth (Fig. 24) (single tooth on paired claw of legs I–III in *C. varvarti* and *C. birmanica*; row of teeth in *C. taiwanensis*).

Etymology.—The species is derived from the Sanskrit word *vali* meaning wrinkle, as one of the characteristic features of this spiders is its heavily wrinkled abdomen.

Description of female holotype.—Total length, 11.30; carapace 5.92 long, 5.54 wide; chelicerae 1.76 intact. Abdomen 5.38 long, 4.4 wide. Spinnerets: PMS, 0.8 long, 0.3 wide, 0.5 apart; PLS, 1.5 total length (0.7 basal, 0.3 middle, 0.5 distal;

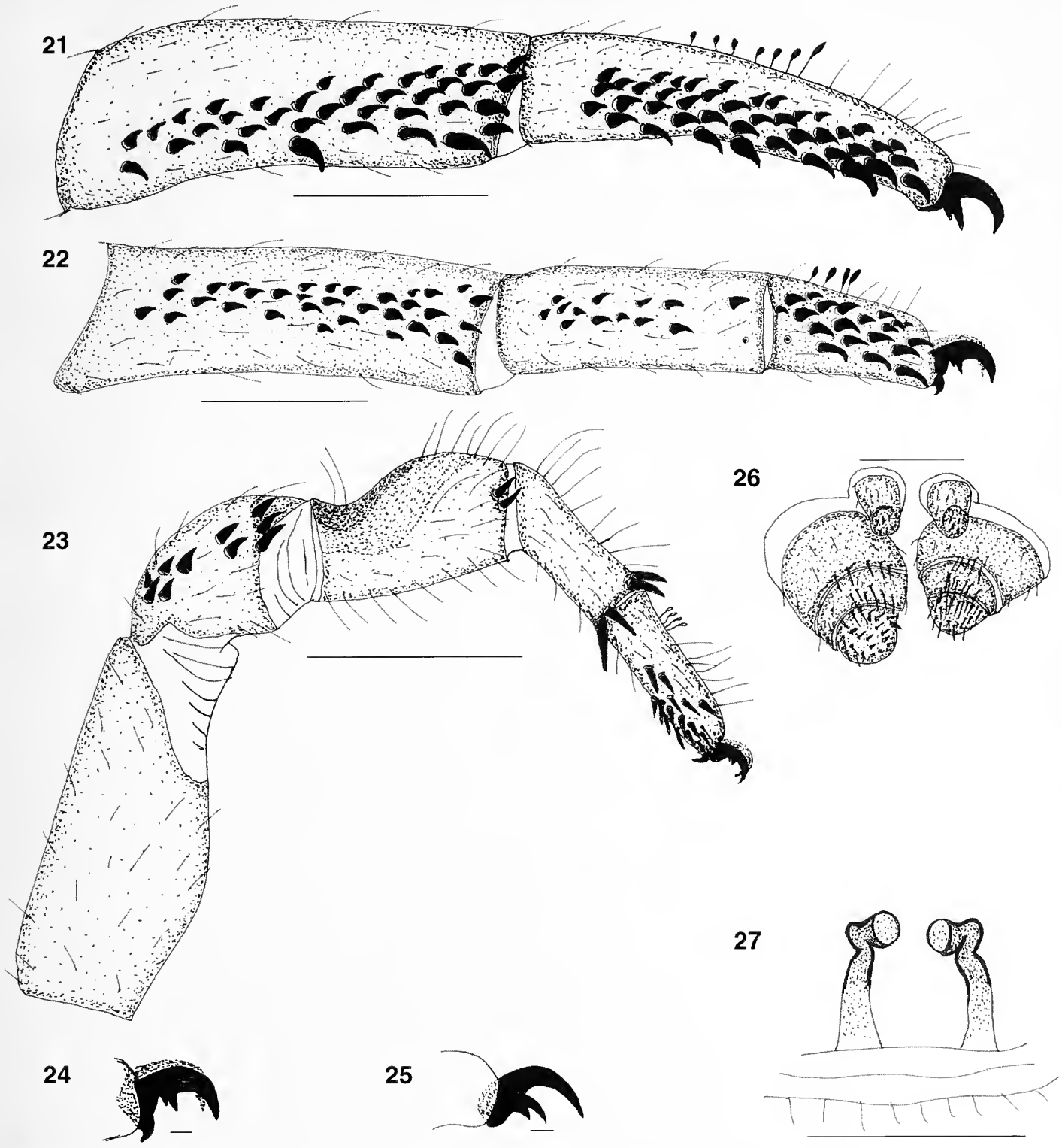


Figures 16–20.—*Conothele vali* new species, female: 16. Cephalothorax and abdomen, dorsal view; 17. Cephalothorax, lateral view; 18. eyes; 19. Sternum, labium, maxillae and chelicerae; 20. Chelicerae, rastellum, promarginal and retromarginal teeth. Scale = 1.0 mm.

midwidths 1.1, 0.9, 0.7 respectively). Morphometry of legs and palp is given in Table 2.

Carapace: reddish-brown, glabrous; black with net-like design, more prominent on the posterior half; thin black band present at periphery; few lines of depression along the interstitial ridges (Fig. 16), weak crenulations on caput, more conspicuous anteriolaterally and near eye region, elsewhere absent or inconspicuous. Caput with distinct mound between fovea and eyes, about twice higher than eyes (Figs. 16, 17). Fovea deep, procurved, U-shaped (Fig. 16). Bristles: 3 long and 18 short ones on caput; one long at anterior edge of ocular tubercle; 2 long and 2 short ones on clypeal plate.

Eyes (Fig. 18): eight in 2 rows, both rows slightly procurved; ocular group 1.0 long, 1.4 wide, about 0.4 of headwidth.



Figures 21–27.—*Conothele vali* new species, female: 21. Tibia and tarsus of palp, retrolateral view; 22. Leg I (tibia to tarsus), prolateral view; 23. Leg III (femur to tarsus), prolateral view; 24. Claw of leg I; 25. Claw of palp; 26. Spinnerets; 27. Spermathecae. Scale = 1.0 mm (Figs. 21–23, 26, 27); 0.1 mm (Figs. 24, 25).

Diameter AME 0.4, PME 0.2, ALE 0.6, PLE 0.3; distance between ALE–AME 0.15, AME–AME 0.1, PLE–PME adjacent, PME–PME 0.5, ALE–ALE 0.7, ALE–PLE 0.2; MOQ not square, 0.8 long, 0.8 front width, 1.0 back width; clypeus 0.7 high.

Maxillae (Fig. 19): 1.8 anterior length, 2.5 posterior length, 1.4 wide; cuspule numbers not same on right and left maxillae, right maxillae with 3 small ones on prolateral-proximal corner, 26 large ones ventrally in ¾ of length, left maxillae with 3 small ones on prolateral-proximal corner, 28 large ones ventrally in ¾ of length. Anterior lobe absent or greatly reduced.

Labium (Fig. 19): 0.9 long, 1.3 wide, shallow labiosternal groove slightly concave; a pair of rectangular black patches

Table 2.—Morphometry of legs and palp of holotype female (WILD-05-ARA-77) of *Conotele vali* new species.

	Leg I	Leg II	Leg III	Leg IV	Palp
Femur	4.12	3.58	3.22	4.1	3.48
Patella	2.30	2.30	2.14	2.24	2.32
Tibia	2.68	2.34	2.08	2.82	2.54
Metatarsus	2.06	1.56	1.74	2.56	-
Tarsus	1.24	1.34	1.88	1.52	2.28
Total	12.4	11.12	11.06	13.24	10.62
		Midwidth			
Femur	0.88	0.9	1.48	0.9	0.9
Tibia	1.0	0.9	0.98	0.9	1.14

covers basal ¼ of labium and labiosternal groove; 8 large cuspules in 2 rows (6 in anterior row and 2 behind centrally), size of cuspules similar to that of maxillae.

Chelicerae (Fig. 20)*:* 3 large and one small promarginal teeth, 6 large and 2 very small retromarginal teeth, basomesal teeth absent; rastellum conspicuous, raised on a low mound, consist of 14 thick spines on vertical face and up, with 8 in anterior row; many long and short spines present along entire anterior dorsal surface.

Sternum (Fig. 19)*:* broader posteriorly, reddish-brown, elevated anterior and lateral sides, sloping posteriorly, 3.22 long, 3.34 wide, covered with long black hair, more towards lateral sides, posterior angle blunt and not separating coxae IV. Sigilla large, irregular shape, centrally placed. Non-sigillate area with fine corrugations.

Legs: all legs similar in thickness, reddish-brown above and light yellowish-brown below except tarsi of palp and metatarsi and tarsi of all legs that are dark brown above and reddish-brown below. Tibiae, metatarsi and tarsi of leg I–II and tibiae and tarsi of palp dorsoventrally flattened. Femora III clearly wider than rest. Tibia III with saddle-shape depression on basal upper part. Metatarsi of leg I, II, IV longer than tarsi. Metatarsal preening combs on all legs absent. Coxae of legs yellowish-brown ventrally. Legs covered with sparsely distributed hair, bristles and few curved thick thorn-like spines (Figs. 21–23). Two conspicuous hairless bands running longitudinally on femora, patellae, and tibiae. Scopulae and claw tufts absent on tarsi of all legs and palp. Leg formula 4123.

Spines (Figs. 21–23)*:* curved thick thorn-like spines present on leg I–II and palp, rest normal thick spines, ti I, p = 33, r = 39; mt I, p = 13 + 1 broken, r = 29; ta I, p = 20 + 1 broken, r = 15; ti II, p = 21, r = 13; mt II, p = 23, r = 15, v = 1; ta II, p = 17, r = 9; pa III, p = 10; ti III, p = 2; mt III, p = 2, d = 4, r = 3; ta III, p = 13, r = 6; mt IV, p = 2; ta IV, p = 11, v = 2; palp, pa, p = 1; ti, p = 35, r = 37; ta, p = 44, r = 41.

Trichobothria: mt I–II with 6 filiform trichobothria in two rows in distal half; mt III with 6 short filiform distally; mt IV with 14 short filiform for length; ta I with 5 clavate trichobothria in basal half, 10 filiform in two longitudinal rows; ta II with 5 clavate in basal half, 12 filiform in two longitudinal rows; ta III with 5 clavate in basal 1/4, 18 filiform in two longitudinal rows; ta IV with 4 clavate basal 1/4, 10 filiform in two longitudinal rows; palp, ti with 8 filiform in curved two rows; ta with 9 clavate centrally, 12 filiform in 2 rows in distal half.

Leg coxae: coxa IV slightly wider than III, I and II subequal.

Claws: all legs with three claws, paired claw with two unequal teeth (Fig. 24). Palp with single claw bearing single unequal bifid tooth (Fig. 25).

Abdomen (Fig. 16)*:* grayish-black with few yellow small spots, wrinkled integument, covered with short and long thorn setae and several bristles; one in 6–8 thorns is long and is about twice longer and slightly thicker than the short thorns. Ventrally yellowish-black, uniformly covered with short and long bristles.

Spinnerets (Fig. 26)*:* PMS digitiform covered with brown hair; PLS, covered with brown hair, apical segment dome-shape.

Spermathecae (Fig. 27)*:* globular apical lobe on a stalk, which is bent (almost 45°) twice distally in zigzag manner.

Distribution.—Known only from the type locality, Tawang, Arunachal Pradesh, India

NATURAL HISTORY

The spider was found in the open along a narrow trail and on the ground at about 2000 m above sea level. The habitat around was mostly secondary scrub with few pine trees, *Pinus walichiana*, growing nearby. The burrow of this spider could not be located as the spider was found in the open; probably the burrow was washed away due to the heavy rainfall at that time.

COMMENTS

An important character which distinguishes *Conothele* from *Ummidia* is the presence of a single short tooth on paired claws of legs I–III (Raven 1985). The transfer of *Ummidia taiwanensis* Tso et al. 2003 and *Ummidia fragaria* (Dönitz 1887) to the genus *Conothele* reveals that these species posses more than one dentition pattern on the paired claws of legs I–III, which does not match the generic key. Similarly, *C. vali* new species also possesses two teeth on the paired claws rather than a single tooth as seen in *C. varvarti* new species. The only character which can distinguish *Conothele* from *Ummidia* will be the absence of the notch on trochanters I–II. Therefore, there is a need to revise the diagnosis of genera, and the generic key of the family Ctenizidae.

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ISSR (Inter Simple Sequence Repeats) as molecular markers to study genetic diversity in tarantulas (Araneae, Mygalomorphae)

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Abstract. Although all species of the *Brachypelma* genus are protected under CITES, few studies have been performed on the genetic structure of the populations of these endangered tarantulas. Here we propose, for the first time in spiders, to use ISSR (Inter Simple Sequence Repeat) technique to study the genetic variability of Mexican populations of *Brachypelma vagans* (Ausserer 1875). We used a nonlethal technique to collect samples from six populations in the Yucatan peninsula and we tested seven ISSR primers. Four of these primers gave fragments (bands) that were sufficiently clear and reproducible to construct a binary matrix and determine genetic variability parameters. We revealed a very high percentage of polymorphism ($P = 98.7\%$) the highest yet reported for tarantula spiders. Our results show that the ISSR-PCR method is promising for intraspecific variation of tarantula spiders.

Keywords: ISSR, Theraphosinae, *Brachypelma*, genetic population, Mexican redrump tarantula

Members of the genus *Brachypelma* are charismatic spiders, being colorful, large, and docile (Locht et al. 1999). The pet trade, habitat destruction, high mortality rates as juveniles, and late sexual maturity result in all *Brachypelma* species being listed in Appendix II of CITES. In recent years, efforts have been made to increase knowledge of their ecology (Yáñez & Floater 2000; Machkour-M'Rabet et al. 2005, 2007) and behavior (Locht et al. 1999; Reichling 2000). However, studies to better understand the genetic structure of tarantula populations are essential to assess the conservation status of the genus. Recently, the development of molecular techniques has helped inform conservation strategies.

Here, we focused our effort on *Brachypelma vagans* (Ausserer 1875), which is distributed from Southern Mexico south to Costa Rica (Locht et al. 1999), but has also been recorded outside its natural range in Florida as a result of the release of pet trade animals (Edwards & Hibbard 1999). As with the study of most tarantulas, the biology and ecology of *B. vagans* is poorly known (Carter 1997; Yáñez et al. 1999; Machkour-M'Rabet et al. 2005, 2007) and little information exists on the genetic structure of its populations (Longhorn et al. 2007).

Mitochondrial DNA and allozyme electrophoresis have been used previously to evaluate population genetics in Mygalomorphae (Ramirez & Froehlig 1997; Bond et al. 2001; Pedersen & Loeschcke 2001; Ramirez & Chi 2004; Bond et al. 2006; Arnedo & Ferrández 2007). For the *Brachypelma* genus (Theraphosidae) only one study has been carried out recently (Longhorn et al. 2007), which focused on the genetic structure of two Belizean populations of *B. vagans* using two portions of mitochondrial DNA (partial 16SRNA + tRNA-Leu + partial ND1 and CO1) and one nuclear non-coding gene (ITS-2). This study showed that nuclear markers are relatively invariant across *B. vagans* populations while mitochondrial markers possess sufficient resolution to estimate the genetic structure of this species. However, it has been suggested that alternative sources of nuclear genes could be used to enhance the characterization of population structure in tarantula spiders. In this context, and because no microsatellite primers are available for *Brachypelma*, we here explore the usefulness of a relatively novel technique in animals, Inter Simple Sequence Repeats (ISSR), to discriminate among populations.

Dominant ISSR markers are widely used in the conservation of rare plants (Kothera et al. 2007) and are being increasingly used in animals (Wink et al. 2002; Hoffman et al. 2006; Guicking et al. 2006; Joger et al. 2007), particularly invertebrates (Abbot 2001; Luque et al. 2002; Chatterjee & Mohandas 2003; Hundsdoerfer & Wink 2006; Roux et al. 2007). However, until now, this technique has not been applied to spiders.

The PCR-ISSR method was used here to screen a large part of the genome without prior knowledge of the sequences. This provides highly reproducible results and generates abundant polymorphisms. The great advantage of ISSR is that the primers work universally for many animal and plant species. Consequently, it is not necessary to define PCR primers for each species, unlike microsatellites. Furthermore, ISSR demands fewer experimental steps and is therefore easy to carry out with a low cost-benefit ratio compared with RFLP (Restriction Fragment Length Polymorphism) and results in a higher reliability and repeatability than RAPD (Random Amplification of Polymorphic DNA; Nagaraju et al. 2001; Luque et al. 2002). Absence of a band is interpreted as the loss of a locus through either the deletion of the SSR (Simple Sequence Repeat) site or a chromosomal rearrangement (Wolfe & Liston 1998). ISSR are thus considered and treated as dominant markers (Casu et al. 2005).

The method uses polymerase chain reaction (PCR) with repeat-anchored or non-anchored primers to amplify DNA sequences between two inverted SSR (Zietkiewicz et al. 1994).

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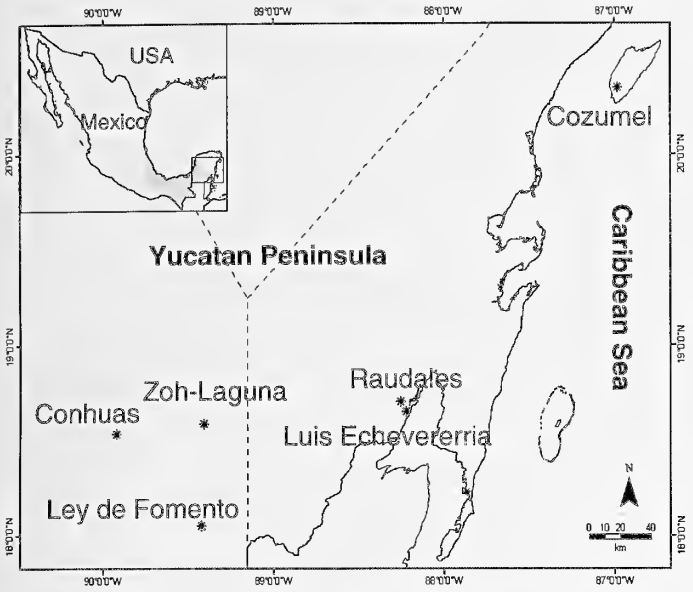

Figure 1.—Location of the six samples used in the study in the Yucatan Peninsula (represented by stars). The geographic distribution of the Mexican Redrump Tarantula, *Brachypelma vagans*, in Mexico is represented on the smaller map (upper left).

Therefore, the only DNA stretches amplified are positioned between two identical but inverted microsatellites (SSR). A single primer can amplify up to 80 loci simultaneously. This method provides genomic information available for a broad spectrum of applications: population genetics, hybridizations, and gene mapping (Wink 2006). The ISSR method represents one of the most promising tools in population genetics studies and deserves increased attention (Behura 2006).

The aim of this study was to technically adapt ISSR-PCR for tarantulas and to provide a preliminary assessment of whether this method is advantageous to explore the genetic structure of tarantula populations. The only previous study using dominant markers (RAPD; Hettle et al. 1997) to study genetic populations of tarantula spiders (*Brachypelma albopilosum* Valerio 1980) showed that none of the six primers used were reliable to differentiate inter- and intra-family relationships. Here we report the technical aspects of a recent molecular tool to study populations of endangered tarantulas.

METHODS

Brachypelma vagans samples were collected during March and April 2007 around six traditional villages of the Yucatan Peninsula (Mexico): Ley de Fomento: 18°03′N, 89°25′W; Conhuas: 18°32′N, 89°55′W; Zoh-Laguna: 18°35′N, 89°24′W; Luis Echevererria: 18°39N, 88°13′W; Raudales: 18°42′N, 88°15′W; and Cozumel: 20°21′N, 86°59′W (Fig. 1). We collected the samples using a nonlethal technique that consists of inducing limb autotomy (Longhorn 2002). In response to pressure, the limb will detach and the muscles will contract to prevent hemolymph loss; spiders in which a limb is removed will regenerate the limb during subsequent molts. We chose to remove the medial limb (III) because the anterior legs (I and II) are used in sensory behaviors and the posterior legs (IV) are used defensively in brushing urticating hairs (Smith 1994). Samples were preserved in 95% ethanol at room temperature, and sent for DNA analysis under CITES export permit (MX34176) to ECOLAB (Laboratoire d'Ecologie Fonctionnelle) at University Paul Sabatier (Toulouse, France).

A small part of the limb was cut off and incubated for 12 h at 50°C in 350 µl of buffer B (10 mM Tris, pH 7.5, 25 mM EDTA, and 75 mM NaCl) with 500 µg of proteinase K and 20 µl of SDS (20%). Proteins and residues were precipitated with 200 µl of saturated NaCl solution and centrifuged at 14,000 rpm for 30 min. DNA from the supernatant was saved and precipitated with 400 µl of cold isopropanol, mixed and centrifuged at 14,000 rpm for 40 min at 2° C. The isopropanol was eliminated and the precipitate was washed with 500 µl of 70% ethanol and centrifuged at 14,000 rpm for 10 min at 2° C. The precipitate was dried and redissolved in 100 µl of TE buffer (pH = 7) and preserved at −28° C until utilization. The concentration of the DNA obtained was determined by spectrophotometry (NanoDrop ND-1000) and the quality was checked using electrophoresis in agarose/TBE (1.2%) gel.

Inter Simple Sequence Repeat (ISSR) analysis was performed using seven primers (Table 1). PCR amplifications were performed in a 25 µl reaction volume containing ~20 ng of template DNA, 50 µM of primer (Invitrogen), 0.2 mM of each dNTP from dNTP Mix (Promega), 2.5 µl of 5× Green Buffer (Promega), 3 µl of $MgCl_2$ (1.5 mM, Promega), and 2.5 U of *Taq* polymerase (Promega). All amplifications were done in a T3 Thermocycler (Biometra). The cycling conditions were as follows: initial denaturation step at 94° C for 4 min, 39 cycles of denaturation at 94° C for 45 s, primer annealing at 56° C for 45 s, and extension at 72° C for 2 min, followed by a final extension at 72° C for 10 min.

Electrophoresis was performed with 7 µl of amplified products on a 2% agarose gel using 1× Tris acetate EDTA buffer at 140 V for ~2 h. The bands were detected with ethidium bromide under UV light and digitized (Bio-Vision 3000, Vilbert-Lourmat) (Figure 2).

In our first experiments, conditions for ISSR with different primers were not optimal. One of the most important factors is

Table 1.—SSR primers screened for ISSR-PCR in the tarantula *Brachypelma vagans*. B = T, C or G; D = A, T or G; R = A or G; Y = C or T; W = A or T.

Code	Sequence (5′→3′)	Abbreviation	Amplification pattern	Total bands
CA	CACACACACACACA	$(CA)_7$	Poor amplification	-
CA+	CACACACACACACARY	$(CA)_7RY$	Smeared	-
+CA	RYCACACACACACACA	$RY(CA)_7$	Smeared with band	-
ACA+	ACAACAACAACAACABDB	$(ACA)_5BDB$	Good	16
+ACA	BDBACAACAACAACAACA	$BDB(ACA)_5$	Good	25
GACA+	GACAGACAGACAGACAWB	$(GACA)_4WB$	Good	15
+GACA	WBGACAGACAGACAGACA	$WB(GACA)_4$	Good	20

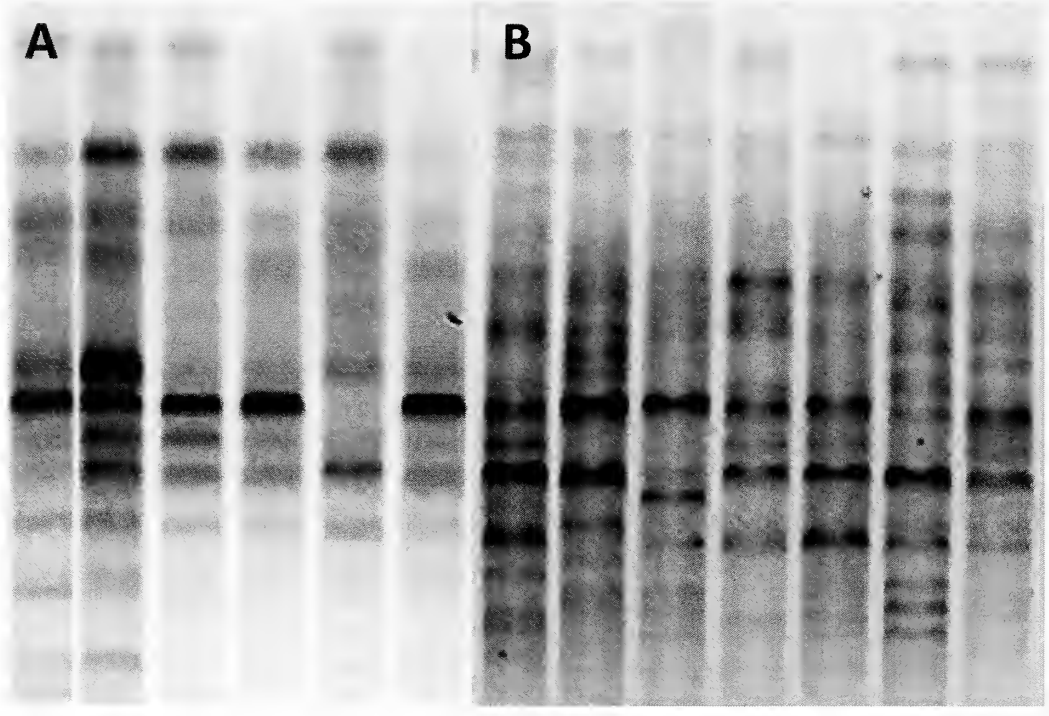

Figure 2.—Example of polymorphic ISSR banding patterns with one marker (+ACA) for two different populations: Cozumel (A) and Luis Echevererria (B).

the difference in the amount of DNA loaded that can weaken the quality of the electrophoretic resolution. In order to obtain comparable and reliable results, we used the same DNA concentration for all samples. We found a minimum optimal amount of 20 ng per sample. Another important parameter is the primer annealing temperature. We experimented with temperatures ranging from 46° C to 66° C with a step of 1° C for all primers and we chose an optimal temperature (56° C) identical for all primers to facilitate the PCR procedure. Also, we checked various parameters to optimize our results. The standard number of reamplifications (39 cycles) was used and gave repeatable and reliable results for all primers. The concentration of $MgCl_2$ was tested from 2.6 µl to 3.4 µl in steps of 0.2 µl and we found good results (quality of the electrophoretic resolution) for values above 3 µl. The concentration of buffer was checked from 2.1 µl to 2.9 µl in steps of 0.2 µl and these modifications had no influence on the results, then we chose a medium value of 2.5 µl. Finally, the method used for storage of the spiders limbs [i.e. preservation in ethanol (95%) and dry-conservation at room temperature (3 years old)], was checked. Only preservation in ethanol resulted in amplification.

The gel separation of ISSR fragments (bands) was used for each individual and each primer to score the presence (1) or absence (0) of bands. This information generated the binary matrix used for analysis. Only bands that could be scored consistently among populations were used, and we assumed that each marker band represented a distinct locus.

The binary matrix was used under Hardy-Weinberg equilibrium to determine the genetic diversity: percentage of polymorphism (*P*), Nei's gene diversity (*h*) using corrected allele frequency (Lynch & Milligan 1994) and the Shannon Index (*H*) (Lewontin 1972), at the species level and for each population. All analyses were carried out using POPGEN Version 1.32 (Yeh et al. 1997). In order to describe the genetic structure and variability among and between populations, non-parametric Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) was performed with GENALEX V6 (9999 permutations; Peakall & Smouse 2006).

RESULTS

Of the seven primers initially tested for the six populations, only four produced clear reproducible fragments (Table 2). Interestingly, the most classic and polymorphic primer (CA_n)

Table 2.—Genetic diversity of *Brachypelma vagans* in the Yucatan Peninsula based on ISSR markers. *n*: number of individuals kept for analysis; N^1: number of bands scored; N^2: number of polymorphic bands; N^3: number of signature bands; *P*: percentage of polymorphism; *h*: Nei's gene diversity; *H*: Shannon Index; SD: standard deviation.

Population name	*n*	N^1	N^2	N^3	*P* (%)	*h* (± SD)	*H* (± SD)
Raudales	22	64	61	1	80.26	0.273 (0.181)	0.411 (0.252)
Zoh-Laguna	24	65	58	0	76.32	0.272 (0.191)	0.405 (0.268)
Ley de Fomento	26	69	64	2	84.21	0.296 (0.178)	0.442 (0.243)
Conhuas	23	65	59	3	77.63	0.271 (0.196)	0.403 (0.270)
Luis Echevererria	26	64	56	1	73.68	0.284 (0.197)	0.418 (0.277)
Cozumel	27	56	43	0	56.58	0.193 (0.203)	0.288 (0.291)

for butterflies (Nagaraju et al. 2001; Luque et al. 2002; Hundsdoerfer & Wink 2006; Roux et al. 2007) failed in the tarantula. From these four primers, a total of 76 scorable ISSR fragments were selected in the 180 individuals screened from all populations (30 individuals for each population). In Table 2, the number of bands and the number of polymorphic bands for each population is given. In addition, we give the number of bands found only within each of the populations, which we call "diagnostic bands" (Table 2; Luque et al. 2002). The very low number of these bands indicates that all populations belong to the same species.

Of the 30 individuals of each population, we only kept individuals presenting a banding pattern for the four primers and for which the interpretation of the banding pattern was unequivocal. For this reason, the number of individuals used for analysis is lower than the number screened (Table 2).

The percentage of polymorphic loci (P) varied between populations (Table 2), ranging from 57% in the Cozumel island population to 84% in the Ley de Fomento population. A mean P of 98.7% was observed across the 6 populations. Nei's gene diversity (h) was low in the Cozumel population with 0.193 (SD = 0.203), while it was higher but relatively constant for continental populations (Table 2). The mean for all populations was 0.324 (SD = 0.164). For the Shannon Index (H), we observed a similar pattern (Table 2): Cozumel island diversity was lower, with a mean across all populations of 0.485 (SD = 0.213).

AMOVA analysis revealed that 79% ($df = 142$, $P < 0.001$) of the variability occurred among individuals within populations and that a strong genetic difference among populations was observed (21%, $df = 5$).

DISCUSSION

Our study revealed a high level of polymorphism for tarantulas in comparison with other studies using allozymes [$P < 7.7\%$ for *Aptostichus simus* Chamberlin 1917 (Cyrtaucheniidae), Ramirez & Froehlig 1997; $P < 33\%$ for *Atypus affinis* Eichwald 1830 (Atypidae), Pedersen & Loeschcke 2001; $P < 30\%$ for *Antrodiaetus riversi* (O. Pickard-Cambridge 1883) (Antrodiaetidae), Ramirez & Chi 2004 (reported therein as *Atypoides riversi*)]. However, the allozyme technique is known to detect a low level of polymorphism with regard to other molecular techniques, and underestimate gene variation (Lowe et al. 2004). Genetic diversity values obtained in our study are congruent with a species having open populations and ample distribution with high gene flow probabilities (Roux et al. 2007; Bouzid et al. 2008).

Consequently, the choice of appropriate molecular markers is very important to study genetic variation at the intraspecific level. In the present study, all mainland populations presented high and similar levels of polymorphism and gene diversity coefficients, whereas the island population of Cozumel presented the lowest values. Generally founded from a small number of individuals (founder effect), island populations usually present less genetic diversity than mainland populations and are often inbred (limited gene flow) (Frankham et al. 2005). However, the values of the Cozumel population did not indicate a threatened population and suggest recent colonization of the island, or an ancient colonization with the occasional introduction, most likely by man, of new individuals from the mainland that can decrease the genetic drift effect.

This study clearly showed the potential of ISSR markers to evaluate genetic diversity in tarantula spiders, and proved an attractive alternative to other molecular markers.

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On the Mediterranean species of Trachelinae (Araneae, Corinnidae) with a revision of *Trachelas* L. Koch 1872 on the Iberian Peninsula

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Abstract. The genus *Trachelas* from the Iberian Peninsula is revised. A new species, *Trachelas ibericus* from Spain, is described from both sexes, and the female of *T. validus* Simon 1884, an Iberian endemic, is described for the first time. Data are presented for the occurrence of *T. canariensis* Wunderlich 1987 and *T. macrochelis* Wunderlich 1992, formerly considered Canarian endemics, on the Iberian Peninsula. *Trachelas praestans* (O. Pickard-Cambridge 1911) is synonymized with *Creugas gulosus* Thorell 1878. *Trachelas purus* Kritscher 1969 is synonymized with *T. rayi* Simon 1878, and *T. flavipes* L. Koch 1882 with *T. maculatus* Thorell 1875. A diagnosis, descriptions, illustrations, distribution data, and a key are presented for the eight presently known *Trachelas* species of the Mediterranean region. In addition, an update is given on the presence of *Cetonana laticeps* (Canestrini 1868) in Spain.

Resumen. En este estudio se hace una revisión del género *Trachelas* en la Península ibérica. Se describe *Trachelas ibericus*, con ambos sexos de España; se describe por primera vez la hembra de *T. validus* Simon 1884, endemismo ibérico. Se presentan datos sobre la presencia de *T. canariensis* Wunderlich 1987 y *T. macrochelis* Wunderlich 1992, especies consideradas antes como endemismos canarios, en la peninsula ibérica. Se sinonimiza *T. praestans* (O. Pickard-Cambridge 1911) con *Creugas gulosus* Thorell 1878. Se sinonimiza *T. purus* Kritscher 1969 con *T. rayi* Simon 1878, así como *T. flavipes* L. Koch 1882 con *T. maculatus* Thorell 1875. Una diagnosis, descripciones, ilustraciones, datos de distribución, y una clave de las ocho especies mediterráneas de *Trachelas* conocidas hasta ahora son aportados. Además se aportan datos que clarifican la presencia de *Cetonana laticeps* (Canestrini 1868) en España.

Keywords: *Cetonana*, taxonomy, revision, faunistics, *ibericus*

Trachelas was first mentioned by L. Koch (1866) as a genus in his Drassidae. As Koch did not describe a type species at the time, *Trachelas* remained a *nomen nudum* until 1872 when L. Koch described *T. minor* in O. Pickard-Cambridge (1872).

Simon (1897) attributed *Trachelas* to Clubionidae, in the group Tracheleae of the subfamily Corinninae. This taxonomic entity was created by Karsch (1880) as the subfamily Corinnidae of his family Drassoidae. Petrunkevitch (1928) and Roewer (1955) both follow Simon's assignment of *Trachelas* to Clubionidae: Corinninae. Corinninae was subsequently raised to family rank by Lehtinen (1967).

The morphology as well as the distribution of the four *Trachelas* species cited from the Iberian Peninsula (Cardoso 2004, 2007; Morano 2005) are poorly known. The type species *Trachelas minor* O. Pickard-Cambridge 1872 as well as *T. rayi* Simon 1878 were described for the last time by Simon (1932). The male palpal tibia of *T. rayi* has also been illustrated by Wunderlich (1992). Only the male has been described for *T. validus* Simon 1884, although the type series also contains a female (see below). *Trachelas. flavipes* L. Koch 1882 is only known from a female specimen from the Balearic Islands on which the original description was based (Koch 1882). That specimen has been lost. *Trachelas amabilis* Simon 1878, from Algeria and Tunisia (Simon 1878b; Bonnet 1959), had been cited from Portugal as doubtful (Cardoso 2000; Morano 2005), but was later excluded from the Portuguese catalog (Cardoso 2004) for being alien to the fauna of that country. Neither *T. amabilis* nor *T. validus* have ever been illustrated.

After studying abundant Iberian material of *Trachelas*, we describe both sexes of a new species, *T. ibericus* sp. n., in the present work, as well as, for the first time, the female of *T. validus*. *Trachelas canariensis* Wunderlich 1987 and *T. macrochelis* Wunderlich 1992, formerly believed to be Macaronesian endemics, are reported from the Iberian mainland and North Africa. Both species, as well as *T. minor*, *T. rayi*, and *T. amabilis*, are redescribed. *Trachelas purus* Kritscher 1969 is synonymized with *T. rayi* and *T. flavipes* with *T. maculatus* Thorell 1875. An identification key for adults of the eight species discussed is also presented. Upon revising this tracheline material, an update is given on the presence of *Cetonana laticeps* (Canestrini 1868), type species of the genus *Cetonana* and its only European representative.

METHODS

In total, 242 specimens were studied (62 ♂♂, 180 ♀♀), as described in detail below. The specimens are deposited in the following collections: Muséum national de Ciencias Naturales de Madrid (MNCN); Museum Nationale d'Histoire Naturelle de Paris (MNHN); Royal Belgian Institute of Natural Sciences, Brussels (RBINS); Royal Museum for Central Africa, Tervuren, Brussels (MRAC); Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt a.M. (SMF); Museum of Natural History, Geneva (MHNG); Collection Christophe Hervé (CCH); Collection J. Bosselaers (CJB); Collection Rop Bosmans (CRB); Collection C. Urones, Universidad de Salamanca (CCU); Collection J.M. Alberdi (JMA); Collection J.A. Barrientos, Universidad Autónoma de Barcelona (JAB). Localities cited are grouped by country and province. Geographical coordinates, altitude above sea level, habitat, and capture mode are given when available.

Specimens were studied with Nikon and Euromex binocular microscopes and drawn by making use of an eyepiece grid. Vulvae were cleared in methyl salicylate and observed under a Wild M12 microscope equipped with a drawing tube. All measurements are in mm except when otherwise stated.

Genital terminology follows Bosselaers & Jocqué (2000).

Abbreviations: AER = anterior eye row; ALE = anterior lateral eyes; AME = anterior median eyes; CO = copulatory opening (entrance of ID); do = dorsal; FD = fertilisation duct; fe = femur; hc = hand capture; HT = holotype; ICS = intercoxal sclerites - intercoxal sclerites are six small triangular or elongated sclerites surrounding the sternum, their tips penetrating between the coxae of the legs - they may be free, or fused with the sternum (Bosselaers & Jocqué 2002:fig. 1K); ID = insemination duct; l = length; LOP = *lorum pediculi* - the lorum is a longitudinal sclerite covering the dorsal side of the petiolus - it may be single or composed of two consecutive or juxtaposed sclerites separated by a membrane (Simon 1892:4, figs. 9–14); LT = lectotype; MOQ = median ocular quandrangle; mt = metatarsus; pa = patella; PER = posterior eye row; pl = prolateral; PLE = posterior lateral eyes; PCT = precoxal triangles - precoxal triangles are small triangular sclerites surrounding the sternum, their tips facing the bases of the coxae (Penniman 1985:16) - they may be free, or fused with the sternum (Bosselaers & Jocqué 2002:fig. 1K); PLB = pleural bars - pleural bars are narrow, horizontal sclerites between coxae and carapace, one above each coxa ("pièces épimériennes" of Simon (1892:11, fig. 29)) - they may be fused with each other (Bosselaers & Jocqué 2002:fig. 1P), with intercoxal sclerites, and/or with the carapace; PME = posterior median eyes; PSP = *plagula sternalis postica* - the plagula is a triangular or ribbon-shaped sclerite situated on the ventral side of the petiolus - it may be fused with the sternum (Simon 1892:5, figs. 15–18; Ledoux & Canard 1991:figs. 13,14); pt = pitfall trap; PT = paratype; PTA = prolateral tibial apophysis; rl = retrolateral; RPA = retrolateral patellar apophysis of male palp; RTA = retrolateral tibial apophysis of male palp; sl = sifting litter; sn = sweep net; st = suction trap; ST1 = spermatheca 1 (connected to FD); ST2 = spermatheca 2, an additional sclerotized hollow receptacle, presumably used for sperm storage (von Engelhardt 1910:38); ta = tarsus; ti = tibia, ve = ventral; w = width.

TAXONOMY

Family Corinnidae Karsch 1880

Diagnosis.—A group of generally small to medium-sized, entelegyne, ecribellate, eight-eyed spiders having tarsi armed with two claws and claw tufts. Corinnidae are further characterized by closely adjacent conical anterior spinnerets having a short, rounded and poorly differentiated apical segment. Female posterior median spinnerets have either three large cylindrical gland spigots in a triangle or, in the subfamily Trachelinae, four to five cylindrical gland spigots in two rows (Bosselaers & Jocqué 2002; Jocqué & Dippenaar-Schoeman 2006); female posterior lateral spinnerets have two large cylindrical gland spigots. The bulbus of the male palp usually lacks a median apophysis and the male abdomen has a strong tendency towards sclerotization.

Remarks.—Corinnidae, formerly subfamily Corinninae of "Clubionidae sensu lato" (Petrunkevich 1928; Simon 1897) is generally considered close to Liocranidae (Coddington & Levi 1991; Deeleman-Reinhold 2001). Corinnidae is represented by three subfamilies in the Iberian Peninsula: Castianerinae, Phrurolithinae, and Trachelinae. Trachelinae, encompassing the genera *Cetonana* Strand 1929 and *Trachelas* in the region under study, can be distinguished from other Corinnidae by a strong reduction in the number of normal leg spines (resulting in complete absence in most genera), the presence, at least in males, of blunt ventral leg cusps on the last three apical segments of the anterior legs (Platnick & Shadab 1974a), and female posterior median spinnerets having four to five cylindrical gland spigots in two rows (Bosselaers & Jocqué 2002; Jocqué & Dippenaar-Schoeman 2006). Trachelinae presently encompass eight genera: *Cetonana, Meriola* Banks 1895, *Paccius* Simon 1898, *Spinotrachelas* Haddad 2006, *Thysanina* Simon 1910, *Trachelas, Trachelopachys* Simon 1897, and *Utivarachna* Kishida 1940. Three additional genera have recently been discovered (Haddad & Lyle, in press). The genera *Austrachelas* Lawrence 1938, *Brachyphaea* Simon 1895, *Lessertina* Lawrence 1942, and *Pronophaea* Simon 1897 have erroneously been attributed to Trachelinae in recent publications (Bosselaers & Jocqué 2002; Dippenaar-Schoeman & Jocqué 1997), but belong elsewhere (Chami-Kranon et al. 2007; Haddad 2006; Lyle & Haddad 2006). The placing of Trachelinae in Corinnidae has been disputed: Lehtinen (1967) makes no mention of Trachelinae under his Corinnidae and in a later publication (Lehtinen 1996:402) refers to family Trachelidae, without further justification. Platnick (1975) already states that "It seems unlikely then that either the castianeirines or the corinnines are the sister group of the trachelines." Jocqué & Dippenaar-Schoeman (2006) consider the inclusion of Trachelinae in Corinnidae debatable and Deeleman-Reinhold (2001:255) states "A familial status for the Castianeirinae and the Trachelinae ... would be more satisfactory."

Genus *Trachelas* L. Koch 1872

Type species.—*Trachelas minor* O. Pickard-Cambridge 1872, by original designation.

Diagnosis.—Apart from the three characters described above for the subfamily, *Trachelas* species (Simon 1878a; Platnick & Shadab 1974a, b) are characterized by a convex bulging carapace, eye rows, especially the posterior one, recurved as seen from above, eyes subequal in size or with the subrectangular posterior median eyes slightly larger than the others, anterior legs more robust than posterior legs, especially in males; a male palp with a narrow cymbium and a simple RTA and/or RPA, globose, often almost spherical female spermathecae, and insemination ducts widened and sclerotized towards the copulatory opening.

Description.—The species-rich and widely distributed genus *Trachelas* is heterogeneous and most probably not monophyletic (see remarks below). As a result, it proves impossible to give a detailed generic description which applies to all species. Instead, a generic description applicable to the Mediterranean species is given here.

Small (2–5 mm) spiders. Carapace convex, yellow-brown, reddish brown or chestnut brown, smooth to minutely warty

or rugose. A small but distinct fovea in posterior part of carapace. Chilum single and subtriangular, or absent. PLB a very narrow strip above each coxa, connected with posterior end to blunt subtriangular sclerites situated between coxae. PLB I fused to PLB II, and PLB III fused to PLB IV, resulting in two conseeutive long strips.

Eyes in two transverse rows, both procurved in frontal view and recurved in dorsal view. PME subrectangular, with a pearly lustre, others transparent and shining, AME darker than others. Dark retina of AME restricted to median two thirds. AME circular, ALE and PLE oval. All eyes ringed with black. Eyes either subequal, or median eyes slightly larger than laterals. Eyes in PER more widely spaced than in AER. MOQ wider posteriorly, w > l. Chelicerae colored as carapace, rugose. Cheliceral boss pronounced in most species. Promarginal and retromarginal cheliceral rim each with two or three teeth.

Sternum slightly longer than wide, rounded and shield shaped. ICS and PCT fused to sternum. ICS rather blunt, especially the posterior one (between coxae III and IV). PCT sharply pointed, triangular. LOP hourglass-shaped, consisting of two trapezoidal sclerites connected by a flexible membrane. PSP surrounding ventral half of petiolus, ribbon-shaped or subtriangular. Labium subtriangular, with a thickened anterior rim. Maxillae widened and rounded anteriorly, flat or with a shallow oblique transversal depression.

Legs spineless, but leg cusps are present on ti, mt, and ta of legs I and II in males of some species. Retrocoxal hymen (Raven 1998; Bosselaers & Jocqué 2002:244) absent, trochanters not notched. Tarsi with two claws and claw tufts. Dark ventral terminal preening brush (Bosselaers & Jocqué 2002:246) present on mt III and IV. Leg formula 4,1,2,3 in females, 4,1,2,3 or 1,4,2,3 or 1,2,4,3 in males.

Abdomen oval, longer than wide, brown or grey with a pattern of patches and chevrons, in males often with a dorsal scutum.

Male palp with a narrow cymbium and either a femur with a ventral terminal groove as well as a small, pointed RPA, or a simple RTA. Bulbus oval to pear-shaped, with an anteriorly inserted embolus.

Epigynum poorly sclerotized and semi-transparent in most species, often with an anterior hood and centrally or anteriorly located COs. Vulva with relatively large, anterior ST2 and posterior, thick-walled ST1 consisting of one or two lumina. IDs relatively simple.

Remarks.—*Trachelas* has a worldwide distribution and 88 species are attributed to the genus (Platnick 2008). In addition to those, one new Asian species (Kim & Lee 2008) and several dozen new African species (Lyle 2008) have recently been discovered. However, the genus as presently delimited is far from homogeneous. As Platnick (2000) correctly states, the genus serves as a "wastebasket" group for relatively unmodified trachelines. Recent studies have moved 27 species to *Meriola, Trachelopachys*, or *Utivarachna* (Platnick 2008). Several authors doubt whether the American species remaining in *Trachelas* are congeneric with the type species *T. minor* (Platnick & Ewing 1995; Grismado 2004). Personal observations demonstrated, for example, that New World *Trachelas* species from the *bicolor* group (Platnick & Shadab 1974b), like *T. barroanus* Chamberlin 1925 and *T. triangulus* Platnick & Shadab 1974, have a posteriorly wedge-shaped carapace, as in *Utivarachna* (Deeleman-Reinhold 2001; Chami-Kranon et al. 2007), while all Old World *Trachelas*, as well as some New World species (e.g., the *tranquillus* group) have a posteriorly truncated carapace. On top of that, the boundaries between *Trachelas* as presently delimited and *Cetonana* are no longer obvious. Although some differences between the type species *C. laticeps* and the Mediterranean *Trachelas* species remain valid (see below), a number of general differentiating characters which Simon lists in his keys and diagnosis (1897:184–185, 1932:957) have since proven incorrect: legs I and II of some *Trachelas* species (*T. minor*, *T. macrochelis*) are not more robust as compared to legs III and IV than those of *Cetonana laticeps*; the fovea is not longer (in both genera 1/10 of length of carapace) or situated more posteriorly on carapace (overlap between both genera). The rather more complex genitalia of *C. laticeps* are nevertheless similar to those of some newly described African *Trachelas* (Lyle 2008), as well as to those of a few *Meriola* species. Similar to *Trachelas*, *Cetonana* is not homogeneous: the African species, which have some normal leg spines, most probably are not congeneric with *Cetonana laticeps* (Haddad, pers. comm.), and the same can be assumed for the three remaining neotropical *Cetonana* (Platnick, pers. comm.) as well as for the Oriental *C. orientalis* (Schenkel 1936), whose females have no leg cusps and a vulvar morphology largely different from that of the type species (Paik 1991). However, a rearrangement of both genera will only be possible after a thorough revision, including a cladistic analysis. This task falls outside the scope of the present study.

As far as Palearctic *Trachelas* are concerned, the following species are listed to date (Platnick 2008): six Asian species (*T. acuminus* (Zhu & An 1988), *T. alticolus* Hu 2001, *T. coreanus* Paik 1991, *T. costatus* O. Pickard-Cambridge 1885, *T. japonicus* Bösenberg & Strand 1906 and *T. sinensis* Chen, Peng & Zhao 1995) three Macaronesian species (*T. canariensis*, *T. macrochelis*, and *T. uniaculeatus* Schmidt 1956) and seven Mediterranean species (*T. amabilis*, *T. flavipes*, *T. maculatus*, *T. minor*, *T. purus*, *T. rayi*, and *T. validus*). In addition to these, Platnick (2008) lists *T. praestans* (O. Pickard- Cambridge 1911), a species introduced in Britain and only known from two male specimens captured in 1911 in a greenhouse at Kew Gardens. The species was described as *Corinna praestans* by O. Pickard-Cambridge (1911), and surprisingly transferred to the genus *Trachelas* by Simon (1932). Comparison of O. Pickard-Cambridge's (1911) excellent illustrations with Bonaldo (2000) clearly shows that these specimens belong to *Creugas gulosus* Thorell 1878, and not to *Trachelas* (Bonaldo, pers. comm.). The likewise introduced species *Trachelas uniaculeatus* is of uncertain origins (Wunderlich 1987, 1992) and poorly illustrated (Schmidt 1990; Wunderlich 1992); it will not be further discussed here.

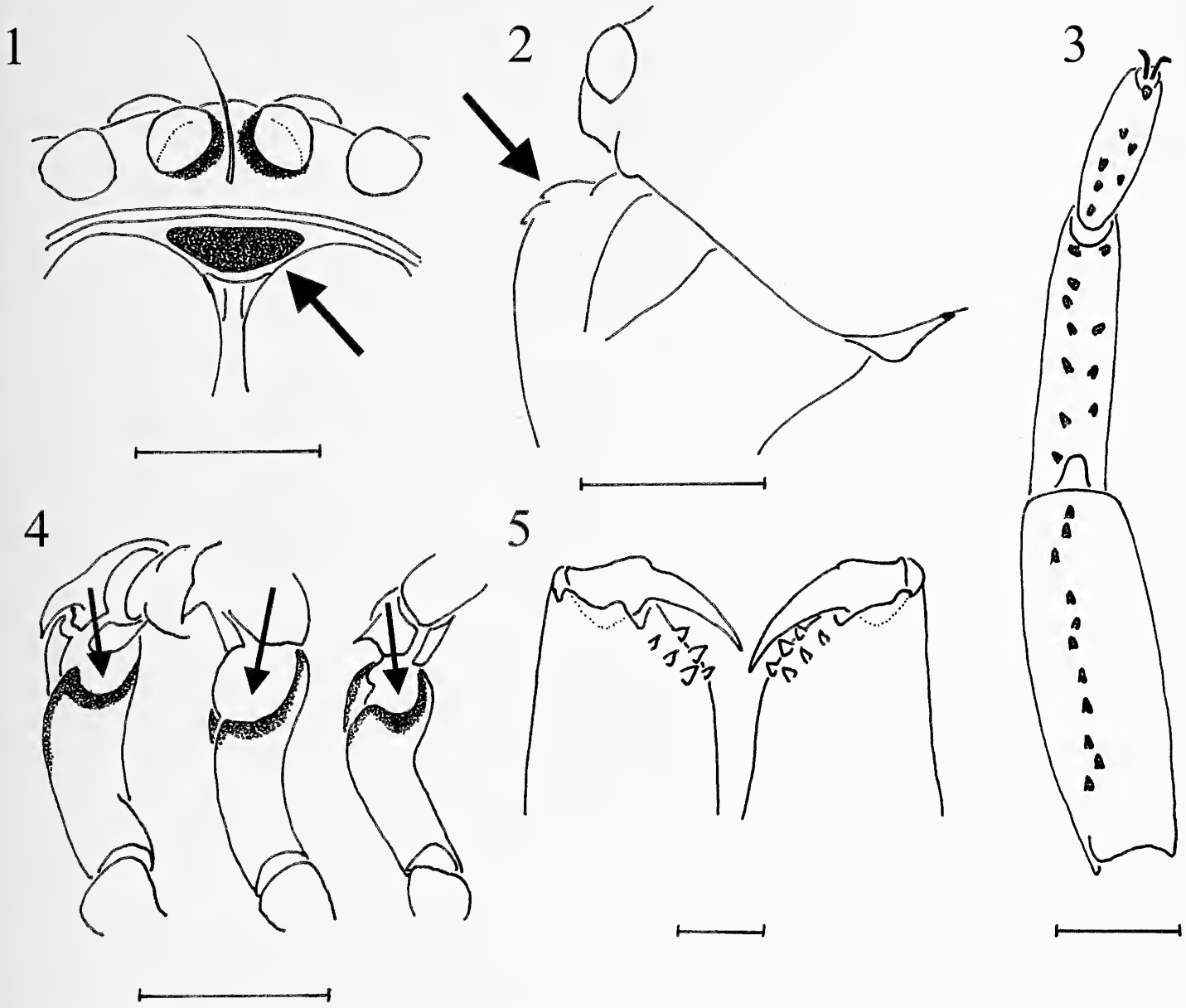
KEY TO IBERIAN *TRACHELAS* SPECIES

1. Males 2
   Females 8
2. Chilum (small sclerite between base of chelicerae and clypeus, Jocqué 1991:11) absent, median eyes further removed from each other than from laterals (Figs. 9, 16, 38), base of chelicerae without pronounced boss, chelicerae with two teeth on both pro- and retromarginal rim, male palpal femur with ventral terminal groove (Fig. 4, arrows; Bosselaers & Jocqué 2002:249), male palpal patella with pointed retrolateral apophysis (Figs. 10, 17, 39), no RTA 3
   Chilum single and sclerotized (Fig. 1), eyes equidistant or medians closer to each other than to laterals, chelicerae with pronounced basal boss (Fig. 2, arrow), promarginal cheliceral rim with three teeth, no palpal femoral groove and no apophysis on male palpal patella, RTA present 4
3. Body length 2 mm or less, leg IV longer than leg I, palpal ventral femoral groove small (Fig. 4, right), embolus short, less than 1/4 of length of bulbus (Fig. 10) ..... *minor*
   Body length 2.5 mm or more, leg I stout and longer than leg IV, palpal ventral femoral groove deep and conspicuous (Fig. 4, left), embolus long, 1/2 of length of bulbus or more (Figs. 17) ..... *canariensis*
4. No leg cusps present, cephalic part of carapace very wide (Figs. 22, 28), 4/5 of carapace width or more, leg II shorter than leg IV 5
   Leg cusps present on at least ti and mt of leg I (Fig. 3), cephalic part of carapace 3/4 of carapace width or less, legs I and II stout, longer than leg IV 6
5. Leg I stout, longer than leg IV, RTA bifid, with blunt tips (Fig. 24) ..... *rayi*
   Leg IV longer than leg I, RTA single, very short and blunt (Figs. 29, 30) ..... *macrochelis*
6. RTA long and pointed, base of tegulum rounded (Fig. 44) 7
   RTA minute and pointed, tegulum with protruding basal bump (Fig. 52) ..... *ibericus*
7. Retromarginal cheliceral rim with two teeth, abdomen without dorsal scutum, RTA more than 4 times as long as wide *maculatus*
   Retromarginal cheliceral rim with three teeth, abdomen with dorsal scutum (Fig. 42), RTA less than 3 times as long as wide (Fig. 44) ..... *validus*
8. Chilum absent, median eyes further removed from each other than from laterals (Figs. 12, 19), base of chelicerae without pronounced boss, chelicerae with two teeth on both pro- and retromarginal rim, no epigynal hood, CO anterior, ST2 spherical (Figs. 15, 21) 9
   Chilum single and sclerotized, eyes equidistant or medians closer to each other than to laterals, chelicerae with pronounced basal boss, promarginal cheliceral rim with three teeth, epigynal hood present (Fig. 32), CO median, ST2 piriform (Fig. 27) 10
9. Body length 2.5 mm or less, first stretch of ID circular (Fig. 15) ..... *minor*
   Body length 2.5 mm or more, first stretch of ID 8-shaped (Fig. 21) ..... *canariensis*
10. Retromarginal cheliceral rim with two teeth, epigynal hood wide (Figs. 25, 32, 35, 40), cephalic part of carapace rather narrow, 2/3 of carapace width 11
    Retromarginal cheliceral rim with three teeth (Fig. 5), epigynal hood narrow and subtriangular (Figs. 45, 54), cephalic part of carapace wide, 3/4 of carapace width 14
11. Epigynal hood medially situated in epigynum, posterior to anterior rim of piriform ST2 (Figs. 26, 32, 36). ST1 dumb-bell-shaped, consisting of two globular, interconnected lumina (Fig. 27) 12
    Epigynal hood anteriorly situated in epigynum, anterior to piriform ST2 (Fig. 40). ST1 sausage-shaped ..... *maculatus*
12. Epigynal hood subrectangular or trapezoidal (Figs. 25, 26) ..... *rayi*
    Epigynal hood curved, arc-shaped (Figs. 32, 35, 36) 13
13. Body size 3.7 mm or less, epigynal hood curved at edges (Fig. 32), lumina of ST1 interconnected by a solenoidally coiled canal (Fig. 33) ..... *macrochelis*
    Body size 3.8 mm or more, epigynal hood crescent-shaped with straight tips (Figs. 35, 36), lumina of ST1 interconnected by a straight canal (Fig. 37) ..... *amabilis*
14. Body size 4 mm or less, epigynum strongly sclerotized with longitudinal median crest, epigynal hood inconspicuous (Figs. 53, 54), ST2 thin-walled, with long stalk (Fig. 55) ..... *ibericus*
    Body size 4.5 mm or more, epigynum weakly sclerotized and semi-transparent, epigynal hood well-defined, narrow and subtriangular (Figs. 45, 46), ST2 thick-walled, with short stalk (Fig. 47) ..... *validus*

Trachelas minor O. Pickard-Cambridge 1872
Figs. 4, 9–15

Trachelas minor O. Pickard-Cambridge 1872:256, pl. 16, fig. 41; Simon 1878a:283; Simon 1897:184, fig. 178; Simon 1932:958, 977, figs. 1498–1499.

Material examined.—SPAIN: *Valencia*, Carlet (39°12′30″N, 0°35′10″W), Orange grove, 160 m, st, 9 September 1999, 1♂ (JAB); 3 November 1999, 1♀ (JAB); 13 April 2000, 1♀ (JAB); Godella (39°31′1″N, 0°24′0″W), Orange grove, 20 m, st, 4 September 2000, 1♂ (JAB); 20 September 2000, 1♂ (JAB); 14 November 2000, 1♂ (JAB); Riola vell (39°10′16″N, 0°20′45″W), Orange grove, 10 m, st, 31 October 2000, 1♀ (JAB); Cheste Hernandina (39°30′15″N, 0°43′25″W), Clementine grove, 270 m, st, 8 September 1999, 1♂ (JAB); 22 September 1999, 1♂ (JAB); 5 October 1999, 1♂, 3♀ (JAB); 10 November 1999, 1♀ (JAB); 26 November 1999, 1♀ (JAB); 14 December 1999, 1♀ (JAB); 4 May 2000, 1♀ (JAB); 6 July 2000, 2♀ (JAB); *Girona*, Mont Ras (41°54′22″N, 3°7′34″E), on bushes near stream bank in cork oak wood, 172 m, sn, 17

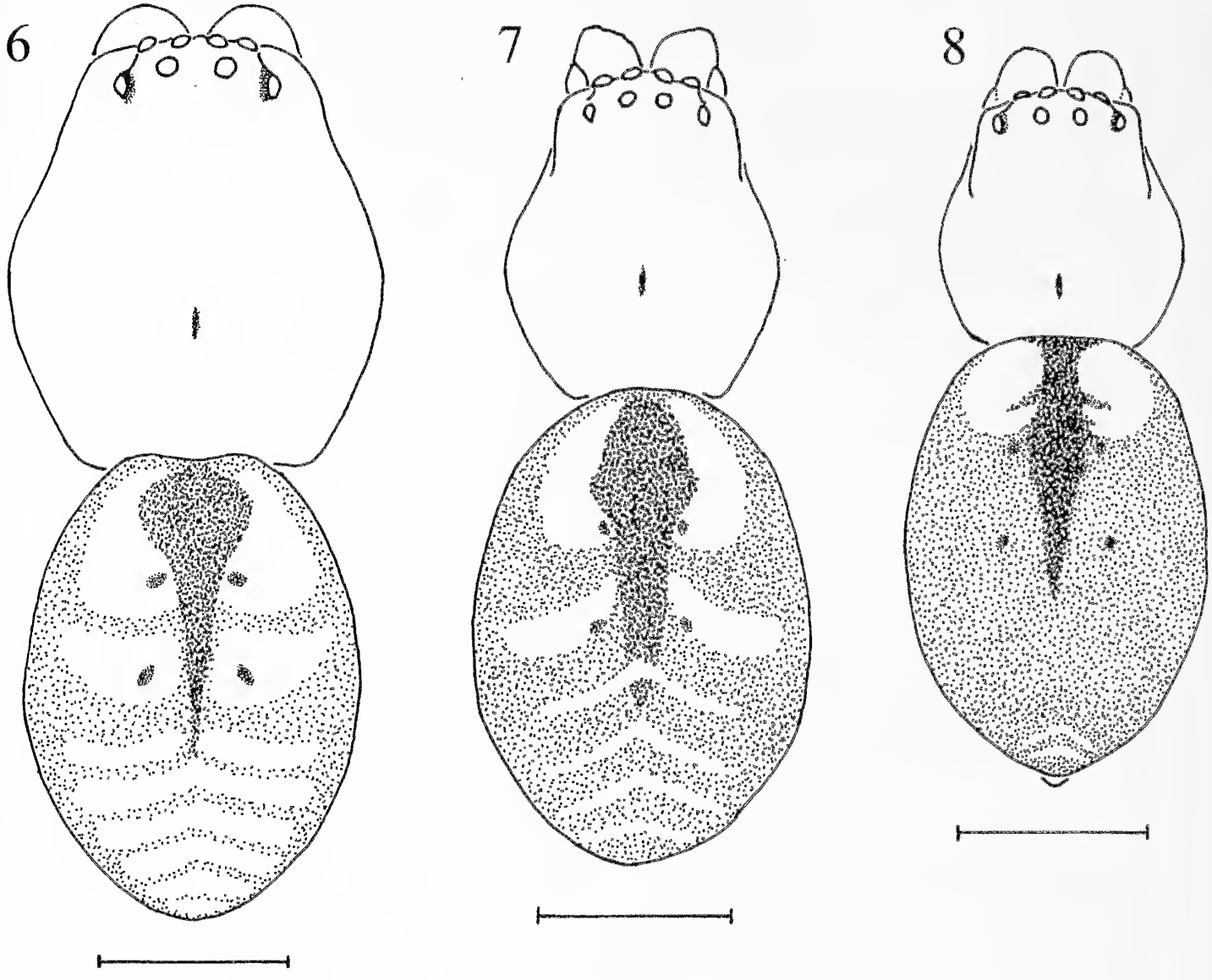


Figures 1–5.—*Trachelas* species. 1–3. *Trachelas ibericus* new species, male: 1. Chilum (arrow); 2. Cheliceral boss (arrow); 3. Ventral view of leg I, with leg cusps. 4. Male palpal terminal ventral femoral groove (arrows): left *Trachelas canariensis*, middle *Trachelas pusillus*, right *Trachelas minor*. 5. *Trachelas validus*: chelicerae with cheliceral teeth, retrolateral view. Scale bars: 1–4: 0.25 mm; 5: 0.5 mm.

April 2003, 1♀ (CJB). PORTUGAL: *Ribatejo*, Santarém, Paul do Boquilobo nature reserve, willow bush, 20 October 2002, P. Cardoso leg., 1♀ (CRB); *Algarve*, Barragem de Beliche, marshy area below dam, with *Typha* sp., 18 February 2006 1♀, (CRB). FRANCE: 2♀ (MNHN-22522); *Bouches-du-Rhône*, 13♂18♀ (MNHN-325); *Corsica*, menhirs de Pelaggiu between Tizzano and Sartenne, in bushes, July 1973, 1♀ (RBINS). GREECE: *Lesbos*, Polychnitos, Aghios Pavlos E., dense *Juncus* vegetation, pt, 10 October 2006, 1♀ (CRB); *Crete*, Chania, Georgiopoli, grassland near marsh, 20 m, 12 September 2004, 1♀ (CRB); Chania, Agia, marshy area around lake, 3 May 2002, 1♀ (CRB); Chania, Frangokastello, dunes with *Phragmites* pools, 10 m, 10 April 2002, 3♀ (CRB); Heraklion, Ano Zaros, Limni Potamou, stones near spring, 370 m, 15 September 2004, 1♂1♀ (CRB); Heraklion, Kasteli N., litter bordering irrigated garden near spring, 19 October 1998, 1♂4♀ (CRB). ALGERIA: *Skikda*, Ben Azouz, moist prairie, 150 m, 23 November 1989, 1♀ (CRB); *El Tarf*, Berrihane, on border between marsh and moist prairie, 30 m, 1 March 1990, 2♀ (CRB); El Kala, Western border of Tonga Lake, moist prairie, 10 m, 27 March 1988, 1♀ (CRB); *Alger*, El Harrach, I.N.A., rough grassland in park, 25 m, pt, 31 December 1985 - 1 June 1986, 1♂1♀ (CRB); *Boumerdes*, Sidi Daoud, Oued Sebaou, alongside Oued, under stones, 35 m, 4 December 1987, 1♀ (CRB).

Diagnosis.—*Trachelas minor* is closest to *T. canariensis*, from which it differs by its smaller size, by its rather short embolus of the male palp (Fig. 10), and by the small COs of the female vulva, connected to thin IDs which are anteriorly looped over 360° (Fig. 15).

Description.—*Male:* Total length 1.80–2.10. Carapace l 1.00, w 0.83, yellowish to reddish brown and densely covered with small, somewhat darker granules carrying diminutive, transparent hairs. Cephalic part narrow (2/3 of carapace width), rounded. Chilum absent.



Figures 6–8.—Dorsal view of *Trachelas* females 6. *T. validus* ; 7. *T. ibericus* ; 8. *T. rayi*. Scale bars: 1 mm.

PME slightly larger than AME, and these in turn larger than the subequal laterals. AME slightly more distant from each other than from laterals, separated by less than one diameter. PME separated by more than one diameter, more distant from each other than from laterals (Fig. 9). Clypeus height slightly larger than diameter of AME.

Chelicerae reddish brown, twice as long as wide, vertical or inclined backwards. Cheliceral boss not very pronounced. Minutely granulated and covered with diminutive, translucent hairs like the carapace. Promarginal and retromarginal cheliceral rim each with two small teeth.

Sternum minutely granulated to almost smooth, light yellow brown with a darker border. PCT weak and sharply pointed, ICS blunt. PSP ribbon-shaped, hemicircular. Labium slightly exceeding 2/3 of maxillae. Maxillae closely appressed to labium, with a shallow oblique transversal depression.

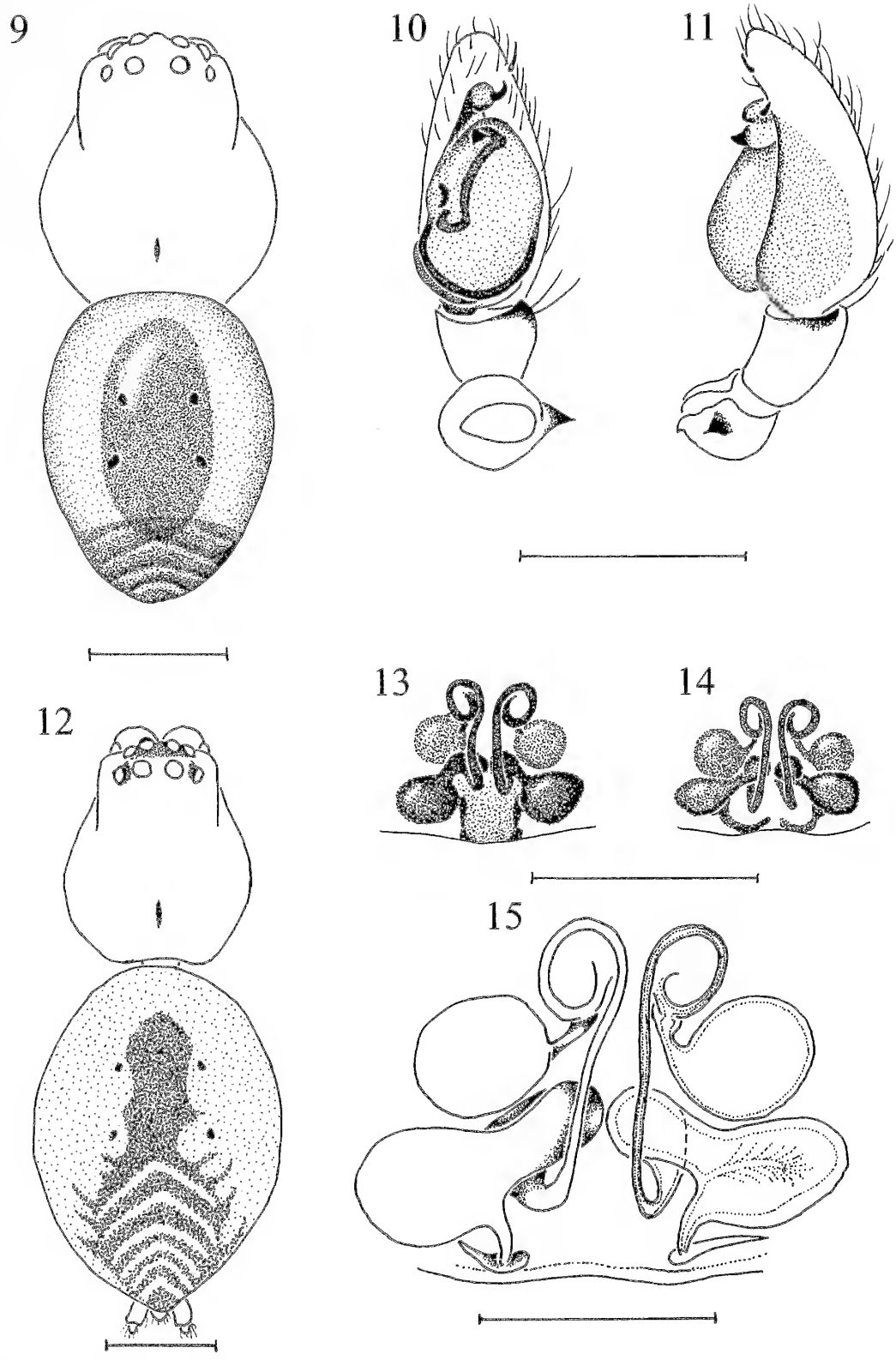
Legs spineless, covered with fine hairs, light yellowish brown, distal segments (pa, ti, mt, ta) somewhat darker than fe. Leg cusps absent. Weak, pale scopulae on all mt and ta and on distal half of ti I and II. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.60	0.24	0.58	0.39	0.34	2.16
II	0.60	0.21	0.53	0.39	0.32	2.05
III	0.45	0.18	0.32	0.39	0.26	1.60
IV	0.66	0.21	0.55	0.58	0.29	2.29

Abdomen pale yellowish grey, with a chocolate brown posterior quarter with thin white chevrons. Narrow, orange-yellow, shining but ill defined dorsal scutum present in central area (Fig. 9).

Male palp with a small, straight and pointed RPA (Fig. 10), less conspicuous than in *T. canariensis* (Fig. 17). RTA absent. Palpal femur with a small, shallow ventral terminal groove (Fig. 4). Bulbus almost completely covering ventral side of cymbium, inflated and wider at base. Curved ducts partly discernable through transparent cuticle. Embolus small (contrary to *T. canariensis*), inserted distally on a small globular excrescence of tegulum, bent, with short, pointed end (Figs. 10, 11).



Figures 9–15.—*Trachelas minor*: 9. Male, do; 10. Left male palp, ve; 11. Left male palp, rl; 12. Female, do; 13, 14. Epigyna, ve; 15. Vulva, ve. Scale bars: 9, 12: 0.5 mm; 10, 11, 13, 14: 0.25 mm; 15: 0.1 mm.

Female: Total length 1.78–2.60. Carapace l 1.09, w 0.88, yellowish to reddish brown, texture as in male. Cephalic part narrow (2/3 of carapace width), rounded. Chilum absent.

Eyes as in male. Clypeus height equal to diameter of AME. Chelicerae, sternum, PSP, labium and maxillae as in male. Legs and leg formula as in male, leg cusps absent.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.66	0.21	0.50	0.37	0.34	2.08
II	0.58	0.21	0.47	0.37	0.29	1.92
III	0.39	0.16	0.32	0.34	0.21	1.42
IV	0.66	0.21	0.58	0.55	0.29	2.29

Abdomen pale yellowish grey, with dark, chocolate brown, lancet-shaped longitudinal median band connected to a concolorous, dark posterior quarter with white chevrons (Fig. 12). Dorsal scutum absent.

Epigynum poorly sclerotized, spermathecae and anteriorly coiled insemination ducts visible through transparent cuticle (Figs. 13, 14). CO anterior.

Vulva (Fig. 15) shows two thin, longitudinally directed, anteriorly coiled IDs running close to the ventral epigynal surface. Immediately behind the anterior CO, a spherical ST2 is attached to the ID by a short duct. Posteriorly, each ID is connected to a piriform ST1. The ST1 is connected to a short, weakly sclerotized caudal FD.

Natural history.—Lives in the bases of grass tufts near rivers (Simon 1878a) and on vegetation, preferably trees and tall herbs (Denis 1933). Our data confirm both habitats; most specimens from Spain were collected on citrus trees with a suction trap; specimens from Greece and Algeria mostly in grassland. Adult females can continuously be found from April to December, while males were mostly captured in Autumn (September to November).

Distribution.—Entire Mediterranean region, eastwards to Azerbaijan, France as far north as Paris, West Africa (Platnick 2008). Existing data for the Iberian Peninsula are scarce. Spain was mentioned by Simon (1932) without precise loeation. One specimen was cited from Portugal (Cardoso 2004). Our data expand the species' range towards the East coast of Spain (Valencia, Girona).

Trachelas canariensis Wunderlich 1987
Figs. 4, 16–21

Trachelas canariensis Wunderlich 1987:238, fig. 636–639; Wunderlich 1992:474.

Types examined.—Paratypes of *Trachelas canariensis* Wunderlich 1987, 3 males, 6 females, Spain, La Gomera, Valle Gran Rey, 28°6'N, 17°16'W, among litter in gully, captured in July, J. Wunderlich leg. (SMF-37310).

Other material examined.—SPAIN: *Galicia*, Campalotra, 18 May 1993, P. Poot leg., 1♀ (CRB); *Almería*, Padules, under stones on dry slope, 9 April 1998, hc, 1♀ (CRB); San Juan de los Terreros, along rivulet near sea, 10 May 1997, pt, 1♀ (CRB). ALGERIA: *Batna*, Ras El Aioun, among grasses around pool in small poplar forest around fountain, 700 m, 16 October 1987, 5♀ (CRB); *Boumerdes*, Reghaia, marsh with Tamarisk at mouth of Oued Reghaia, 5 m, 3 May 1988, pt, 5♀ (CRB); *Aïn Temouchent*, between El Malah and El Ghella, among *Salicornia* and *Atriplex* near brackish water along Rio Salado, 80 m, 24 April 1984, 2♀ (CRB). MOROCCO: *Marrakech*, Oued Tensift near Marrakech, in and along river bed, 9 February 1996, 2♀ (CRB); *Taroudannt*, between Squirate and Taroudannt, litter in flooded *Citrus* yard, 15 February 2007, 1♂2♀ (CRB). TUNISIA: *Gabes*, Arram, among stones and herbs around irrigation canals, 16 December 1999, 1♂3♀ (CRB); Zarat, orchards in oasis, 19 December 2000, 3♂2♀ (CRB). KENYA: *Central Province*, Mt. Kenya, Sirimon track, montane rain forest, 2550 m, 25 July 1975, R. Bosmans leg., 1♀ (MRAC-161902). CONGO: *North Kivu*, Mt. Ruwenzori, North face, Kikura camp, 2000 m, July - August 1974, M. Lejeune leg., 1♀ (MRAC-154732); Kambaila, June 1973, M. Lejeune leg., 1♂1♀ (MRAC-145812); Sake, May 1937, J. Ghesquière leg. 1♂ (MRAC-174292). RWANDA: *Kigali*, Bugesera, borders of lake Tsohoa, September 1957, N. Leleup leg., 1♂ (MRAC-097139); *East Province*, Lulama, Lake Ihema, 6 June 1969, R. Kiss leg., 1♀ (MRAC-159694).

Diagnosis.—*Trachelas canariensis* is closest to *T. minor*, from which it differs by its larger size, by its long and twisted terminally inserted embolus of the male palp (Fig. 17), and by the large COs of the female vulva, connected to widened IDs which are anteriorly bent into an 8-shape (Fig. 21).

Description.—*Male:* Total length 2.42–2.97. Carapace 1 1.24, w 1.05, yellow ochre, covered with small warts carrying diminutive, transparent hairs. Cephalic part narrow (about 2/3 of carapace width), rounded. Chilum absent.

Eyes subequal, AME slightly more than half of their own diameter from each other, 1/4 of their diameter from ALE. PME separated by less than 1.5 of their diameter from each other, and by about 1/2 of their diameter from PLE (Fig. 16). Clypeus height equal to diameter of AME.

Chelicerae yellow brown, minutely granulated and covered with diminutive, translucent hairs, cheliceral boss not very pronounced. Promarginal and retromarginal cheliceral rim each with two small teeth.

Sternum almost smooth, light yellow brown with a darker border. PCT weak and sharply pointed, ICS blunt. PSP ribbon-shaped, hemicircular. Maxillae closely appressed to labium, with a shallow oblique transversal depression.

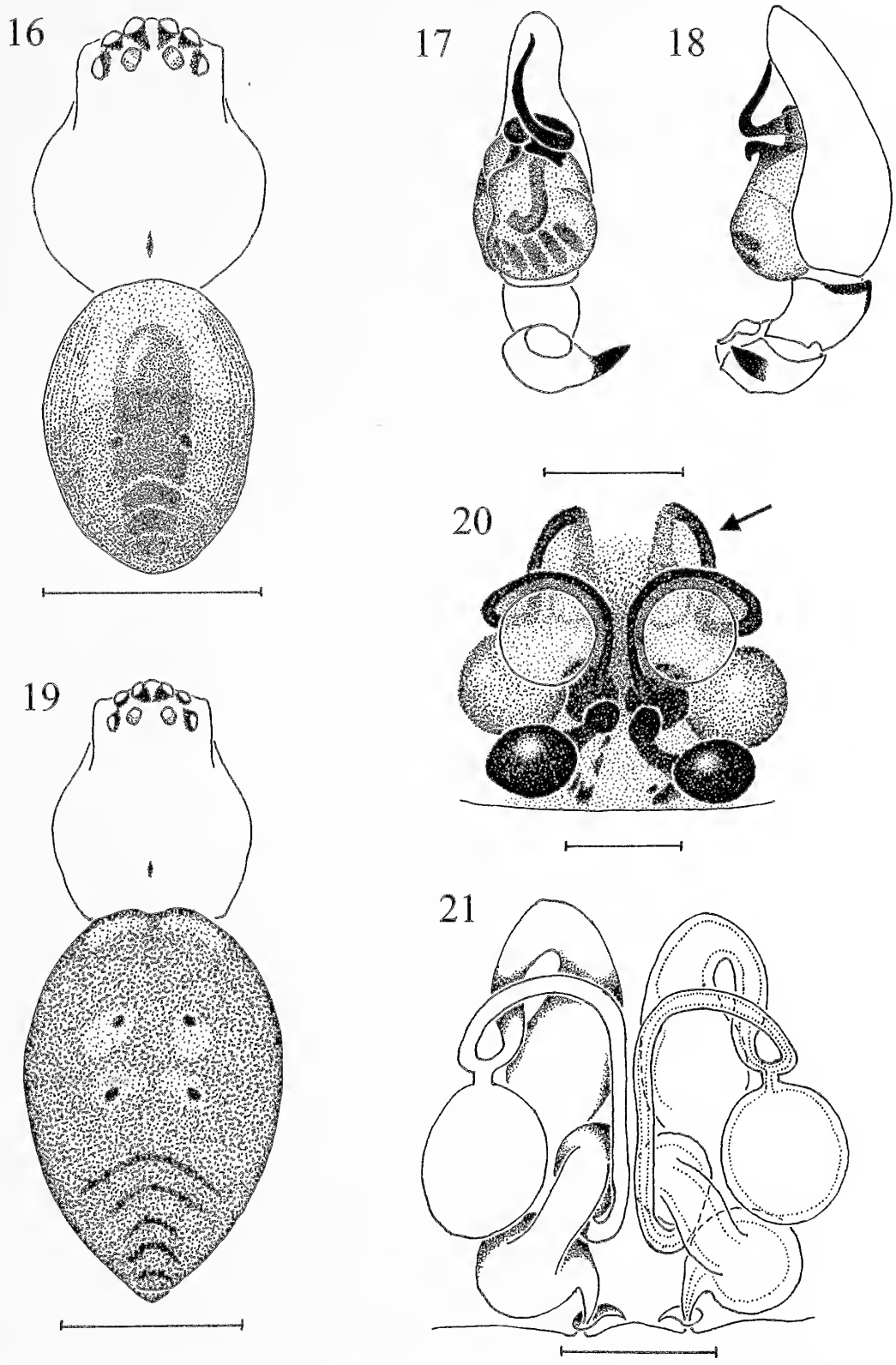
Legs spineless, covered with fine hairs, orange-yellow. Leg cusps absent. Pale scopulae on mt and ta I and II. Leg formula 1,4,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.92	0.34	0.84	0.60	0.45	3.16
II	0.79	0.32	0.74	0.55	0.42	2.81
III	0.60	0.24	0.45	0.47	0.32	2.08
IV	0.79	0.26	0.74	0.74	0.37	2.89

Abdomen cream, posterior quarter darker, with a chocolate brown inverted triangular patch with thin pale transversal chevrons. Narrow, orange-yellow, shining but ill defined dorsal scutum present, which is as long as abdomen but variable in width from lanceolate to oval, covering 30 to 90% of abdomen (Fig. 16).

Male palp with curved and pointed RPA (Figs. 17, 18). RTA absent. Palpal femur with a deep ventral terminal groove (Fig. 4). Bulbus almost completely covering ventral side of



Figures 16–21.—*Trachelas canariensis*: 16. Male paratype, do; 17. Right male palp, ve (inverted); 18. Right male palp, rl (inverted); 19. Female paratype, do; 20. Epigynum, ve; 21. Vulva, ve. Scale bars: 16, 19: 1 mm; 17, 18: 0.25 mm; 20, 21: 0.1 mm.

cymbium, inflated and wider at base. Curved ducts partly discernable through transparent cuticle. Embolus long and coiled, inserted distally on tegulum (Figs. 17, 18).

Female: Total length 2.50–3.37. Carapace l 1.22, w 1.04, orange-yellow, texture as in male. Cephalic part narrow (slightly less than 2/3 of carapace width), rounded. Chilum absent.

PME slightly larger than AME, and these in turn larger than the subequal laterals. AME 2/3 diameter from each other, 1/3 diameter from ALE. PME 1.5 diameter from each other, 2/3 diameter from PLE (Fig. 19). Clypeus height 4/3 of diameter of AME.

Chelicerae, sternum, PSP, labium and maxillae as in male.

Legs as in male, leg cusps absent. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.63	0.26	0.60	0.45	0.37	2.31
II	0.63	0.26	0.55	0.42	0.34	2.21
III	0.53	0.21	0.39	0.42	0.26	1.81
IV	0.95	0.24	0.63	0.66	0.32	2.79

Abdominal pattern variable in intensity: from cream with a dark, chocolate brown posterior zone (as in *T. minor*) to dark greyish-brown with four paler spots around sigilla and a number of thin, dark brown transversal chevrons posteriorly (Fig. 19). Dorsal scutum absent.

Epigynum poorly sclerotized, spermathecae and anteriorly bent insemination ducts visible through transparent cuticle (Fig. 20). Wide and sclerotized CO median-anterior.

Vulva (Fig. 21) shows two thin, longitudinally directed, anteriorly widened and bent IDs running close to the ventral epigynal surface. Immediately behind the wide and sclerotized median-anterior CO, a spherical ST2 is attached to the ID by a short duct. Posteriorly, each ID is connected to a piriform ST1. The ST1 is connected to a short, weakly sclerotized caudal FD.

Distribution.—Formerly considered a Canarian endemic (Platnick 2008; Wunderlich 1987, 1992) this species now proves to have an extremely large distribution area, having been collected in Rwanda, Congo, Kenya, Tunisia, Algeria, Morocco, the Canary Islands, and the Spanish mainland.

Remarks.—Comparison of the rather detailed drawings by Lessert (1923) and Wunderlich (1987) suggests that *T. canariensis* might be a junior synonym of *T. pusillus*. However, after studying the holotype of *T. pusillus* (Figs. 4, 38, 39) it is obvious that both species are different. The holotype of *T. pusillus* has horizontally protruding chelicerae not observed in *T. canariensis*, and the embolus of the male palp is considerably shorter than that of *T. canariensis* (Figs. 38, 39). A pale, ill-defined dorsal scutum covers the entire abdomen of the holotype specimen, and the left palp is missing. The tube containing the holotype of *T. pusillus* is accompanied by a second tube, containing Lessert's original label and a left male palp. This left male palp, surprisingly, turns out to be a palp of *T. canariensis*, not belonging to the holotype of *T. pusillus*.

Over its extended range, *T. canariensis* shows some variablity: the length of the retrolateral patellar apophysis varies to a certain extent, and the width of the anterior part of the epigynum, consisting of the first, forward-directed, and the second, backward-directed stretch of the ID continuously varies from narrow, with an almost straight second stretch (Fig. 20, arrow), to almost as wide as the ST2 region, with a semi-circular second stretch.

Trachelas rayi Simon 1878
Figs. 22–27

Trachelas rayi Simon 1878a:284, pl. 16, fig. 1; Simon 1932:959, figs. 1500, 1501; Wunderlich 1992:475, fig. 740.

Trachelas purus Kritscher 1969:306, fig. 11, NEW SYNONYMY.

Material examined.—SPAIN, FRANCE: (no locality specified, label only mentions "Gallia. Hisp."), 6♂43♀ (MNHN-1523). SPAIN: *Cádiz*, Tarifa, April 1991, P. Poot leg., 1♀ (CRB). FRANCE: *Var*, Caillan, 1♀ (MNHN-4.25.9.62, Collection Berland); Île de Port Cros, 1♀ (MNHN); *Alpes Maritimes*, Ste Agnès, 14 March 1914, 1♀ (MNHN-878); *Pyrenées Orientales*, Cerdagne, August 1978, L. Baert leg., 1♀ (CRB). ALGERIA: *Bouira*, Ighrem, under tamarisk along Oued Sahel river, 490 m, 10 June 1989, pt, 1♂1♀ (CRB).

Diagnosis.—*Trachelas rayi* is closest to *T. macrochelis*, from which it differs by its abdominal pattern consisting of a dull grey background featuring two large pale patches in the frontal half and a number of thin white chevrons in the posterior quarter, by its male palp with a blunt, bifid RTA and a very short, blunt apical embolus (Fig. 23), and by its epigynum which is bordered by a narrow, notched anterior hood (Figs. 25, 26).

Description.—*Male:* Total length 2.40–3.10. Carapace l 1.39, w 1.21, reddish brown to chestnut brown. Top almost smooth, sides covered with small warts carrying diminutive, transparent hairs. Cephalic part wide (4/5 of carapace width), rounded and bulging (Fig. 22). Chilum single, sclerotized, reddish brown.

Eyes subequal, AME separated by less than one diameter, closer to each other than to laterals. Eyes of PER widely and equidistantly spaced, separated by about two diameters (Fig. 22). Clypeus height slightly smaller (0.8) than diameter of AME.

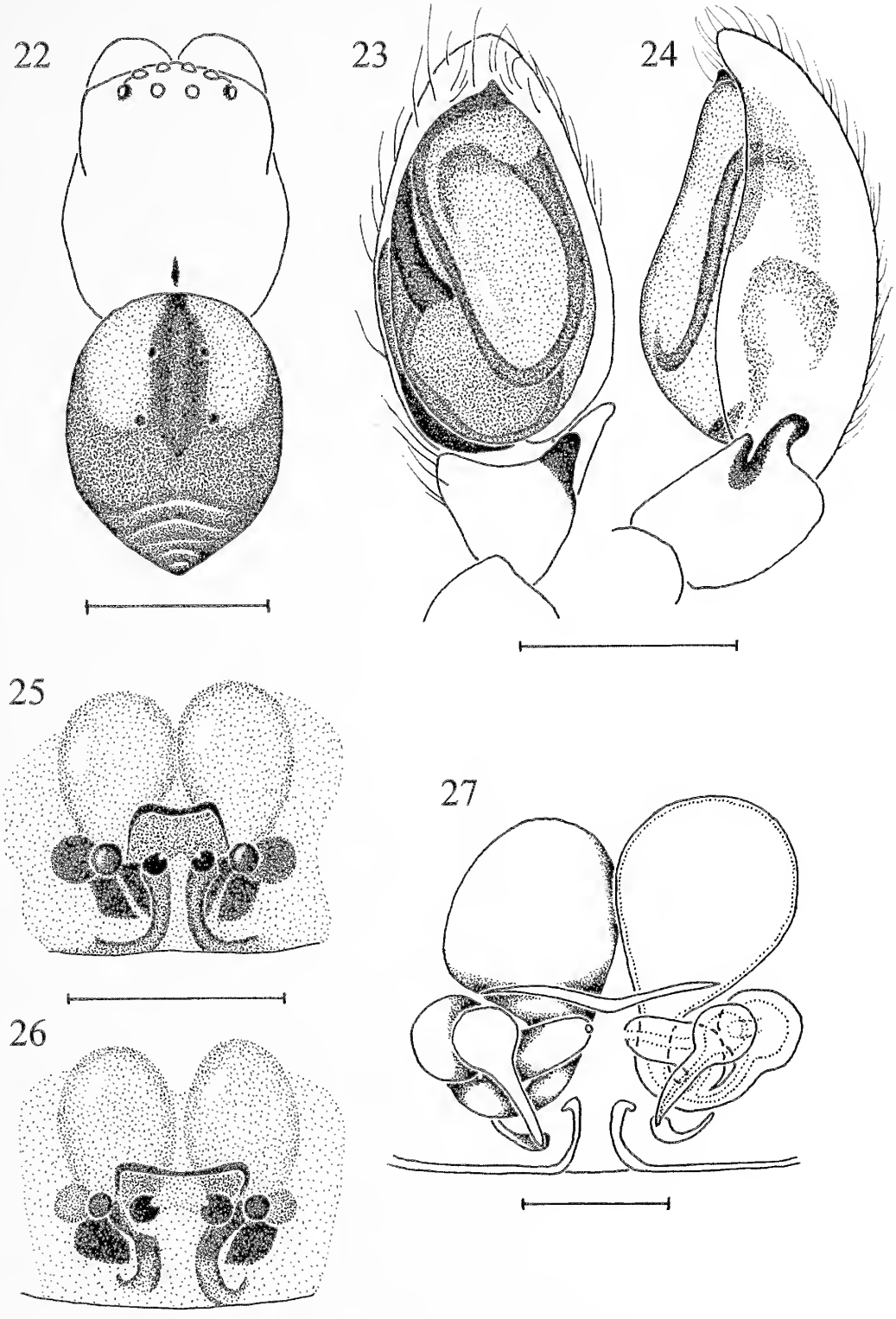
Chelicerae chestnut brown, rugose. Cheliceral boss very pronounced: anterior base of chelicerae protruding almost horizontally. Promarginal rim with three teeth, increasing in size towards fang base, retromarginal rim with two subequal teeth.

Sternum smooth with some isolated small pits, yellow brown with a darker border, which is almost obscuring the weak, pointed PCT. ICS blunt. PSP ribbon-shaped, hemicircular. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II ochre, legs III and IV pale yellow. Leg cusps absent. Dense ventral scopulae consisting of erectile bristles on ta, mt and ti I and II. Ventral terminal preening brush on mt III and IV sparse. Leg formula 1,4,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.89	0.37	0.79	0.47	0.34	2.87
II	0.74	0.32	0.55	0.39	0.34	2.34
III	0.53	0.24	0.39	0.47	0.24	1.87
IV	0.79	0.29	0.60	0.74	0.26	2.68



Figures 22–27.—*Trachelas rayi*: 22. Male, do; 23. Left male palp, ve; 24. Left male palp, rl; 25, 26. Epigyna, ve; 27. Vulva, ve. Scale bars: 22: 1 mm; 23–26: 0.25 mm; 27: 0.1 mm.

Abdomen grey with a longitudinal, dagger-shaped dark grey mark enclosed between two oval white patches in anterior half and 4–6 thin, transversal white chevrons in posterior quarter (Fig. 22). Dorsal scutum absent.

Male palp with bifid RTA, consisting of a short, subtriangular ventral part and a longer, recurved and blunt dorsal part (Fig. 24). Bulbus oval, with a short and blunt apical embolus. Sperm ducts partly discernable through transparent cuticle (Figs. 23, 24).

Female: Total length 2.60–3.70. Carapace l 1.40, w 1.24, reddish brown, entirely covered with small warts carrying diminutive, transparent hairs. Cephalic part slightly wider than 2/3 of carapace width. Chilum single, sclerotized, brown.

Eyes as in male. Clypeus height smaller (0.6) than diameter of AME.

Chelicerae structured and toothed as in male, but cheliceral boss somewhat less pronounced.

Sternum smooth with some isolated small pits, brown with darker, thickened border. PCT pointed, more conspicuous than in male. PSP subtriangular, with a blunt tip directed towards sternum. Labium as long as wide. Maxillae without oblique depression.

Legs as in male, all femora paler than distal articles. Leg cusps absent. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	0.92	0.39	0.79	0.58	0.39	3.08
II	0.84	0.37	0.66	0.53	0.37	2.76
III	0.66	0.26	0.53	0.53	0.26	2.24
IV	0.92	0.37	0.79	0.89	0.34	3.31

Abdomen oval, colored as in male (Fig. 8). Dorsal scutum absent.

Epigynum poorly sclerotized, with a central depression anteriorly bordered by a narrow, arc-shaped hood enclosing the two dark, sclerotized COs. The large, anteriorly situated, piriform ST2 are clearly visible through the transparent cuticle (Figs. 25, 26).

Vulva (Fig. 27) shows two large piriform ST2 anterior to a thin, arc-shaped epigynal hood. Immediately posterior to the hood are the medially situated COs and the first stretch of the ID, which is directed outward, then bent in caudal direction and splitting in a wide duct towards ST2 and a narrower one, directed outward and connecting to the dumb-bell-shaped, posterolaterally situated ST1. ST1 consists of two globular, interconnected lumina. The smaller, ventral lumen is connected to the long, tapering FD, the larger dorsal one communicates with the ID.

Natural history.—Lives on sunny slopes in open vegetation and vineyards. Often found among dry leaves and in pruning litter (Simon 1878a).

Distribution.—France, Italy (Platnick 2008, Trotta 2005). Was cited from the Iberian Peninsula by Cardoso (2004): Val do Guadiana nature reserve, Serpa, one specimen on *Cystus* sp., 120 m. Our data establish the presence of *T. rayi* in Spain and Algeria.

Remarks.—*Trachelas purus*, only known from a single female collected on bushes on 6 September 1960 in Chioggia, Italy; has never been collected again. The type specimen could not be obtained, but Kritscher's description (Kritscher 1969) is fully compatible with all characteristics of *T. rayi*, a species which has been reported from Italy (Trotta 2005). Kritscher's poor drawing of the epigynum is quite similar to the epigynum of *T. rayi*, with the large anterior ST2, smaller lateral ST1 and a central depression enclosing the COs. *Trachelas purus* is herewith synonymized with *T. rayi*.

Trachelas macrochelis Wunderlich 1992
Figs. 28–33

Trachelas macrochelis Wunderlich 1992:474, figs. 733–739.

Types examined.—Holotype, 1 male, Spain, Canary Islands, Hierro, La Dehesa, July (no year indicated on label), J. Wunderlich leg. (SMF-37153).

Other material examined.—SPAIN: *Cádiz*, Tarifa, March 1991, P. Poot leg., 1♀ (CRB); Torre de la Higuera, dunes, among stones and debris, 9 April 1994, 4♀ (CRB); *Almería*, Cabo de Gata, small bushes in dunes, 10 m, 6 April 1997, 1♀ (CRB). ALGERIA: *Djelfa*, Djelfa, Dj. Djellal, *Pinus halepensis* forest, 1310-1400 m, pt, 1990-1991, 1♀ (CRB).

Diagnosis.—*Trachelas macrochelis* is closest to *T. rayi*, from which it differs by the very large male chelicerae, by its abdominal pattern consisting of a dark grey-green background featuring four ill-defined pale patches in the anterior half and a number of thin white chevrons in the posterior half, by its male palp with a very short and blunt RTA and a short, pointed and retrolaterally curved apical embolus (Fig. 29), and by the epigynum being anteriorly bordered by a wide, semicircular, laterally curled hood (Fig. 32).

Description.—*Male:* Total length 2.95. Carapace l 1.47, w 1.16, orange brown, slightly rugose. Cephalic part wide (almost 9/10 of carapace width), rounded and bulging. Chilum single, sclerotized, orange.

All eyes subequal, eyes in AER equidistant, separated by one diameter. Eyes of PER also equidistantly spaced, separated by slightly less than two diameters (Fig. 28). Clypeus height 3/4 of diameter of AME.

Chelicerae orange, very large, cheliceral boss very pronounced: anterior base of chelicerae protruding almost horizontally. Promarginal rim with three teeth, increasing in size towards fang base, retromarginal rim with two teeth.

Sternum smooth, greyish yellow with a darker border, which largely obscures the small, pointed PCT. ICS blunt. PSP subtriangular, with a blunt tip directed towards sternum. Labium slightly longer than wide, 3/4 of maxilla length. Maxillae without oblique depression.

Legs spineless, orange, covered with fine hairs. Leg cusps absent. Ventral scopulae on ta and mt I and II, almost none on ti I and II. Ventral terminal preening brush on mt III and IV brownish. Leg formula 4,1,2,3.

Leg measurements:

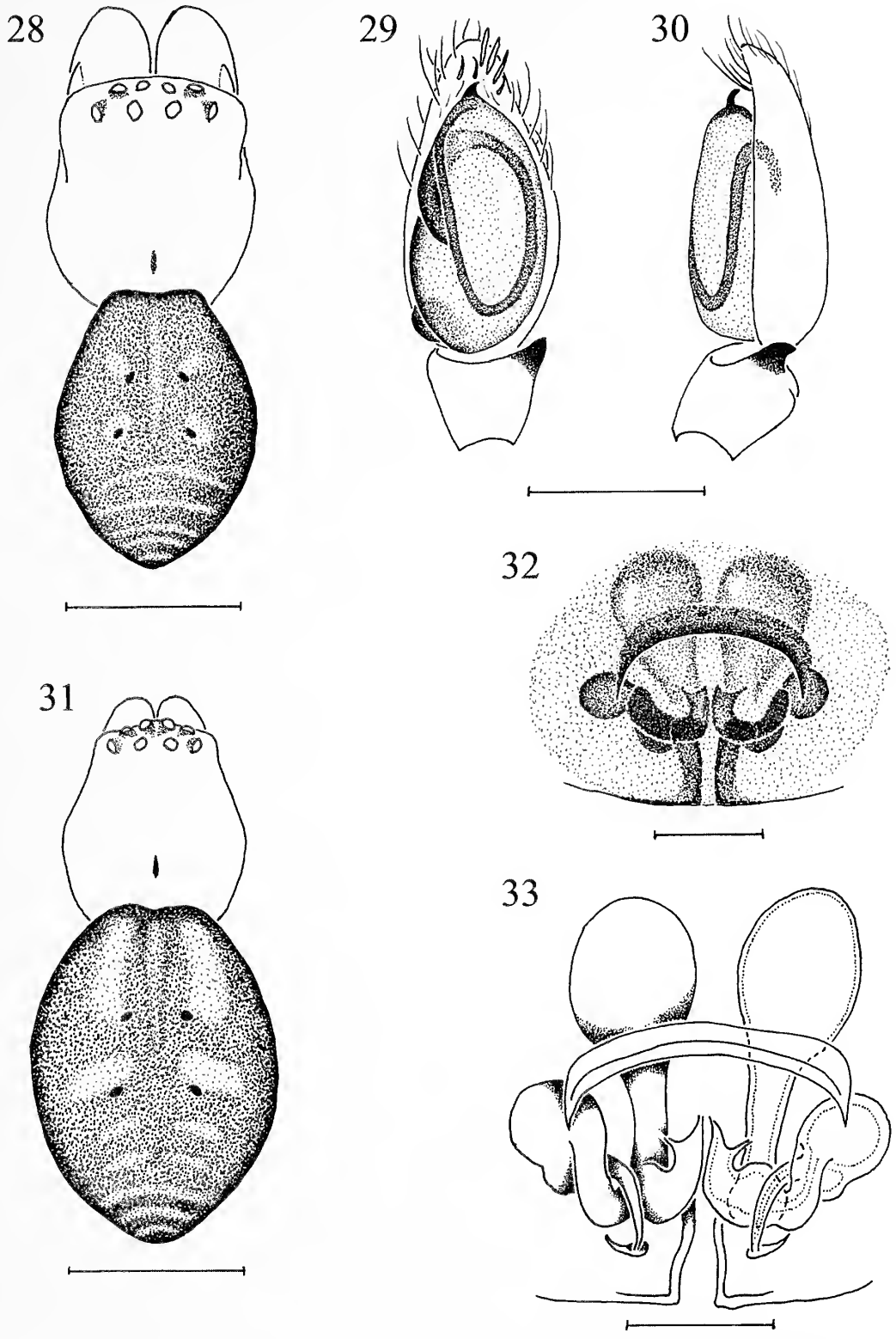
	fe	pa	ti	mt	ta	total
I	0.84	0.32	0.66	0.55	0.39	2.76
II	0.76	0.32	0.58	0.50	0.34	2.50
III	0.63	0.29	0.45	0.50	0.24	2.10
IV	0.87	0.34	0.63	0.79	0.26	2.89

Abdomen greyish green with four ill-defined paler patches surrounding sigilla in anterior half and 5-6 thin, transversal pale chevrons in posterior half (Fig. 28). Dorsal scutum absent.

Male palp with very short and blunt RTA (Fig. 29). Bulbus oval, with a short, pointed and retrolaterally curved apical embolus. Sperm ducts partly discernable through transparent cuticle (Figs. 29, 30).

Female: Total length 2.84–3.71. Carapace l 1.26, w 1.08, brown, almost smooth, cephalic part about 2/3 of carapace width. Chilum single, sclerotized, brown.

All eyes subequal, AME separated by one diameter from each other and by 2/3 diameter from ALE. Eyes of PER



Figures 28–33.—*Trachelas macrochelis*: 28. Male holotype, do; 29. Right male palp, ve (inverted); 30. Right male palp, rl (inverted); 31. Female, do; 32. Epigynum, ve; 33. Vulva, ve. Scale bars: 28, 31: 1 mm; 29, 30: 0.25 mm; 32, 33: 0.1 mm.

equidistantly spaced, separated by about 1.5 diameters (Fig. 31). Clypeus height 2/3 of diameter of AME.

Chelicerae yellow-brown, granulated, structured and toothed as in male, but smaller and with a less pronounced cheliceral boss.

Sternum smooth, brown with darker, thickened border. PCT small and sharply pointed, ICS blunt. PSP as in male. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II orange, legs III and IV orange-yellow. Leg cusps absent. Ventral

scopulae consisting of erectile bristles on ta, mt, and ti I and II. Leg formula 4,1,2,3.

Leg measurements:

	Fe	pa	ti	mt	ta	total
I	0.87	0.34	0.76	0.58	0.42	2.97
II	0.79	0.32	0.66	0.55	0.37	2.68
III	0.58	0.24	0.39	0.53	0.26	2.00
IV	0.92	0.32	0.74	0.84	0.32	3.13

Abdomen dark greenish grey with two pear-shaped pale patches followed by two transversal light patches in anterior half and 5-6 pale, thin transversal chevrons in posterior half (Fig. 31). Dorsal scutum absent.

Epigynum poorly sclerotized, with a central depression anteriorly bordered by a wide, semicircular hood enclosing two small, centrally located COs connected with the clearly visible lateral, circular ST1 by a conspicuous, dark brown ID. The large, anteriorly situated, piriform ST2 are partly visible through the transparent cuticle (Fig. 32).

Vulva (Fig. 33) shows two large piriform ST2 anterior to a thin, ellipsoidal, laterally curved epigynal hood. Immediately posterior to the hood are the medially situated COs and the first stretch of the ID, which is directed outward, widened halfway and splitting in an anteriorly directed duct towards ST2 and an outwards oriented one connecting to the laterally situated ST1, which consists of two globular lumina interconnected by a solenoidally coiled canal. The posterior lumen of ST1 is connected to a long and thin FD.

Distribution.—Not a Macaronesian endemic as stated by Wunderlich (1992) and Platnick (2008). Our data expand the species' range to the Iberian mainland and Algeria.

Trachelas amabilis Simon 1878
Figs. 34–37

Trachelas amabilis Simon 1878b:50.

Types examined.—Lectotype (designated here), 1 female, specimen in separate glass microtube, Algeria, Oran, Daya, 36°7'N, 0°20'E; paratypes: 3 females, 2 juveniles Algeria, Oran, Daya; Tunisia, Mahadia, no additional details on label (MNHN-1784).

Other material examined.—ALGERIA: *Boumerdes*, Reghaya, dunes near shore, 5 m, 31 October 1985, 1♀ (CRB). TUNISIA: *Gafsa*, Lidillat, 1 juv., "Auct. det." (MNHN).

Diagnosis.—*Trachelas amabilis* is closest to *T. macrochelis* from which it differs by its larger size and by its abdominal pattern, consisting of a dark purplish brown background with a longitudinal, dagger-shaped black mark flanked on each side by two oval cream patches in the anterior half and followed by 5–7 wide, transversal cream chevrons in the posterior half (Fig. 34), and by the epigynum which is bordered by a wide, anterior arc-shaped hood that is not laterally curled (Figs. 35, 36).

Description.—*Male:* unknown.

Female: Total length 3.80–5.20 (LT 4.65). Carapace l 1.97, w 1.58, chestnut brown, entirely covered with small warts carrying diminutive, transparent hairs. Cephalic part slightly wider than 2/3 of carapace width. Chilum single, sclerotized, brown.

All eyes subequal, AME separated by less than one diameter, closer to each other than to ALE. Eyes of PER equidistantly spaced, separated by 1.5 diameters (Fig. 34). Clypeus height smaller (0.7) than diameter of AME.

Chelicerae brown, rugose. Cheliceral boss pronounced, anterior base of chelicerae protruding almost horizontally. Promarginal rim with three teeth, diminishing in size towards cheliceral base, retromarginal rim with two subequal teeth.

Sternum smooth with some isolated small pits, brown with darker, thickened border. PCT sharply pointed, ICS blunt. PSP subtriangular, with a blunt tip directed towards sternum. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, orange yellow. Leg cusps absent. Dense ventral scopulae consisting of erectile bristles on ta, mt and ti I and II. Ventral terminal preening brush on mt III and IV sparse. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	1.32	0.53	1.03	0.82	0.53	4.21
II	1.16	0.47	0.92	0.76	0.47	3.79
III	0.92	0.39	0.60	0.76	0.34	3.02
IV	1.32	0.47	1.03	1.18	0.39	4.39

Abdomen dark purplish brown with a longitudinal, dagger-shaped black mark flanked on each side by two oval cream patches in anterior half and followed by 5–7 wide, transversal cream chevrons in posterior half (Fig. 34). Dorsal scutum absent.

Epigynum poorly sclerotized, with a central depression anteriorly bordered by a wide, semicircular hood enclosing the two dark, sclerotized COs. The large, anteriorly situated, piriform ST2 are clearly visible through the transparent cuticle (Figs. 35, 36).

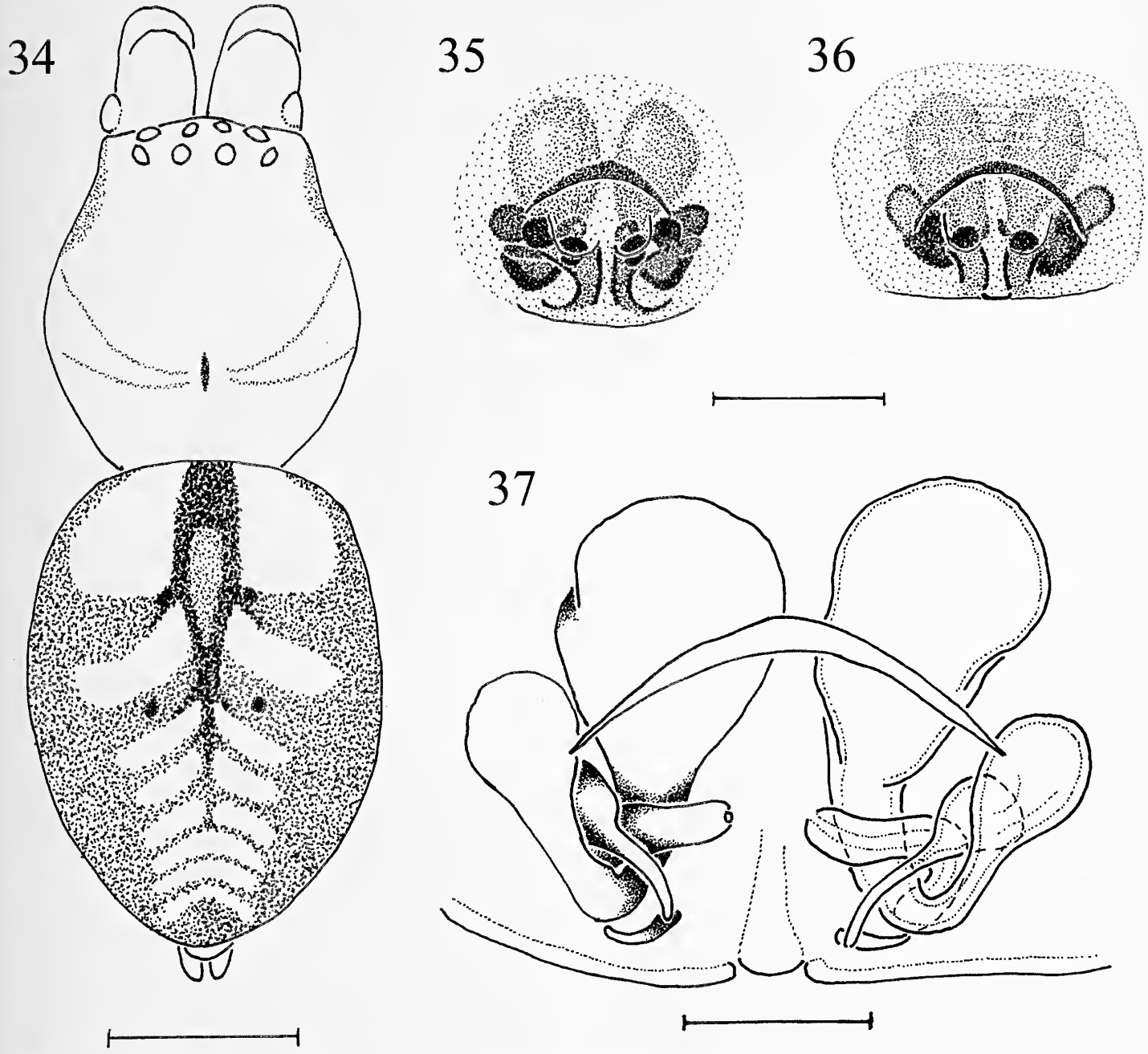
Vulva (Fig. 37) shows two large piriform ST2 anterior to a thin, arc-shaped epigynal hood. Immediately posterior to the hood are the medially situated COs and the first stretch of the ID, which is directed outward, then bent in caudal direction and splitting in a wide duct towards ST2 and a narrower one, directed outward and connecting to the dumb-bell-shaped, posterolaterally situated ST1. ST1 consists of two globular, interconnected lumina. The smaller; dorsal lumen is connected to the long and thin FD, the larger ventral one communicates with the ID.

Distribution.—Algeria, Tunisia (Platnick 2008). The present data confirm the known range of the species. *Trachelas amabilis* has not yet been found on the Iberian Peninsula, but is included in the present revision because of the close proximity of its distribution area to the region of interest.

Trachelas maculatus Thorell 1875
Figs. 40, 41

Trachelas maculatus Thorell 1875a:77;
Thorell 1875b:87; Chyzer & Kulczyński 1897:253, pl. 10, fig. 15; Mikhailov 1987:1583, figs. 1, 2.
Trachelas flavipes Koch 1882:638, pl. 20, figs. 17, 18, NEW SYNONYMY.

Material examined.—FRANCE: *Paris*, Parc de Bercy, Le Labyrinthe et Le Jardin Aromatique, sn, 23 October 2004, 1♀ (CCH).



Figures 34–37.—*Trachelas amabilis*: 34. Female lectotype, do; 35, 36. Epigyna, ve; 37. Vulva, ve. Scale bars: 34: 1 mm; 35, 36: 0.25 mm; 37: 0.1 mm.

Diagnosis.—*Trachelas maculatus* is closest to *T. validus*, from which it differs by its grey abdomen having four vague, irregular pale patches in the frontal half, the pale patches revealing an underlying pattern of tiny, dark grey spots (Fig. 41), by a male palp with a thin hemicircular apical embolus, and by the epigynal depression which is bordered by a wide, arched anterior hood situated anterior to the large piriform ST2 (Fig. 40).

Description.—(Translated and adapted from Chyzer & Kulczyński 1897 and Mikhailov 1987)

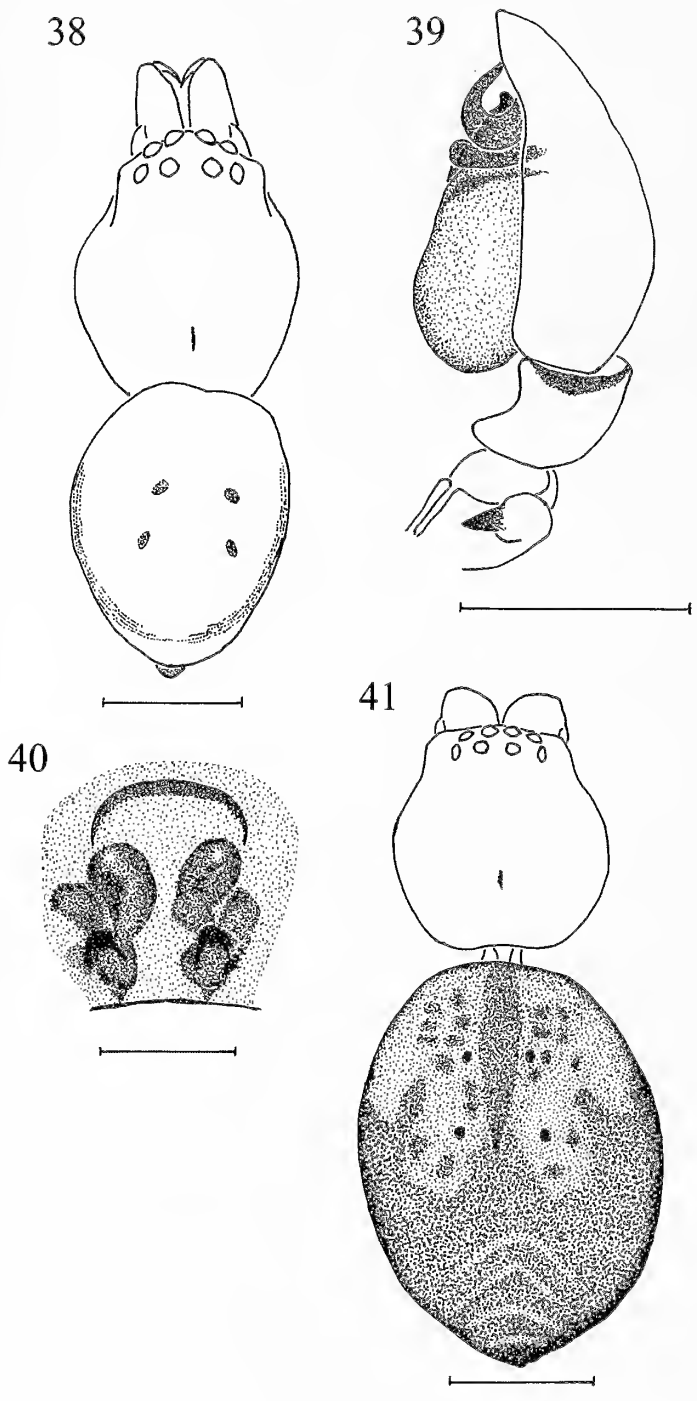
Male: Total length 4.10. Carapace l 1.95, w 1.71, light chestnut brown, with small pronounced pits. Cephalic part slightly wider than 2/3 of carapace width.

Eyes of AER subequal and equidistant, separated by less than one diameter. Eyes of PER also subequal and equidistant, separated by somewhat less than two diameters. Eye diameter in AER 5/6 of eye diameter in PER.

Chelicerae chestnut brown, rugose. Cheliceral boss very pronounced: anterior base of chelicerae protruding almost horizontally. Promarginal rim with three, retromarginal rim with two teeth.

Sternum light chestnut brown, slightly pitted.

Legs spineless, orange brown, femora of anterior legs darker. Tarsi with two claws and claw tufts. Ti and mt I with ventral leg cusps (Platnick & Shadab 1974, Platnick & Ewing 1995). Leg formula 1,2,4,3.



Figures 38–41.—*Trachelas* species. 38, 39. *Trachelas pusillus*: 38. Male holotype, do; 39. Right male palp, rl (inverted). 40, 41. *Trachelas maculatus*: 40. Epigynum, ve; 41. Female, do. Scale bars: 38: 0.5 mm; 39, 40: 0.25 mm; 41: 1 mm.

Leg measurements:

	Fe	pa	ti	mt	ta	total
I	1.77	0.78	1.47	1.16	0.65	5.82
II	1.48	0.62	1.29	1.06	0.60	5.04
III	1.01	0.47	0.72	0.86	0.42	3.48
IV	1.27	0.59	1.13	1.24	0.48	4.69

Abdomen grey with two large, irregular light spots anteriorly and two transversal median light patches.

Male palp with long, pointed and dorsally recurved RTA. Bulbus oval, with a thin and pointed apical embolus describing a hemicircle. Ventrally appressed to the embolus is a transparent apophysis which can be considered a functional conductor. Sperm ducts partly discernable through transparent cuticle.

Female: Total length 3.88. Carapace l 1.88, w 1.65, colored and textured as in male. Cephalic part slightly wider than 2/3 of carapace width.

All eyes subequal, Eyes of AER separated by less than one diameter, eyes of PER separated by about 1.5 diameters (Fig. 41).

Chelicerae brown, structured and toothed as in male, but cheliceral boss somewhat less pronounced.

Sternum smooth with some isolated small pits, orange brown with darker, thickened border. PCT and ICS strongly sclerotized and pointed, except ICS III, which is blunt. PSP subtriangular. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, legs I and II orange brown, legs III and IV yellow. Leg cusps absent. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	1.40	0.69	1.07	0.93	0.64	4.73
II	1.29	0.66	1.07	0.97	0.57	4.56
III	0.97	0.54	0.74	0.83	0.40	3.48
IV	1.36	0.64	1.21	1.31	0.50	5.02

Abdomen grey with two large, irregular light spots anteriorly, two transversal median light patches and a number of thin transversal chevrons in posterior part (Fig. 41). The four large, pale patches reveal an underlying pattern of tiny, darker grey spots. Dorsal scutum absent.

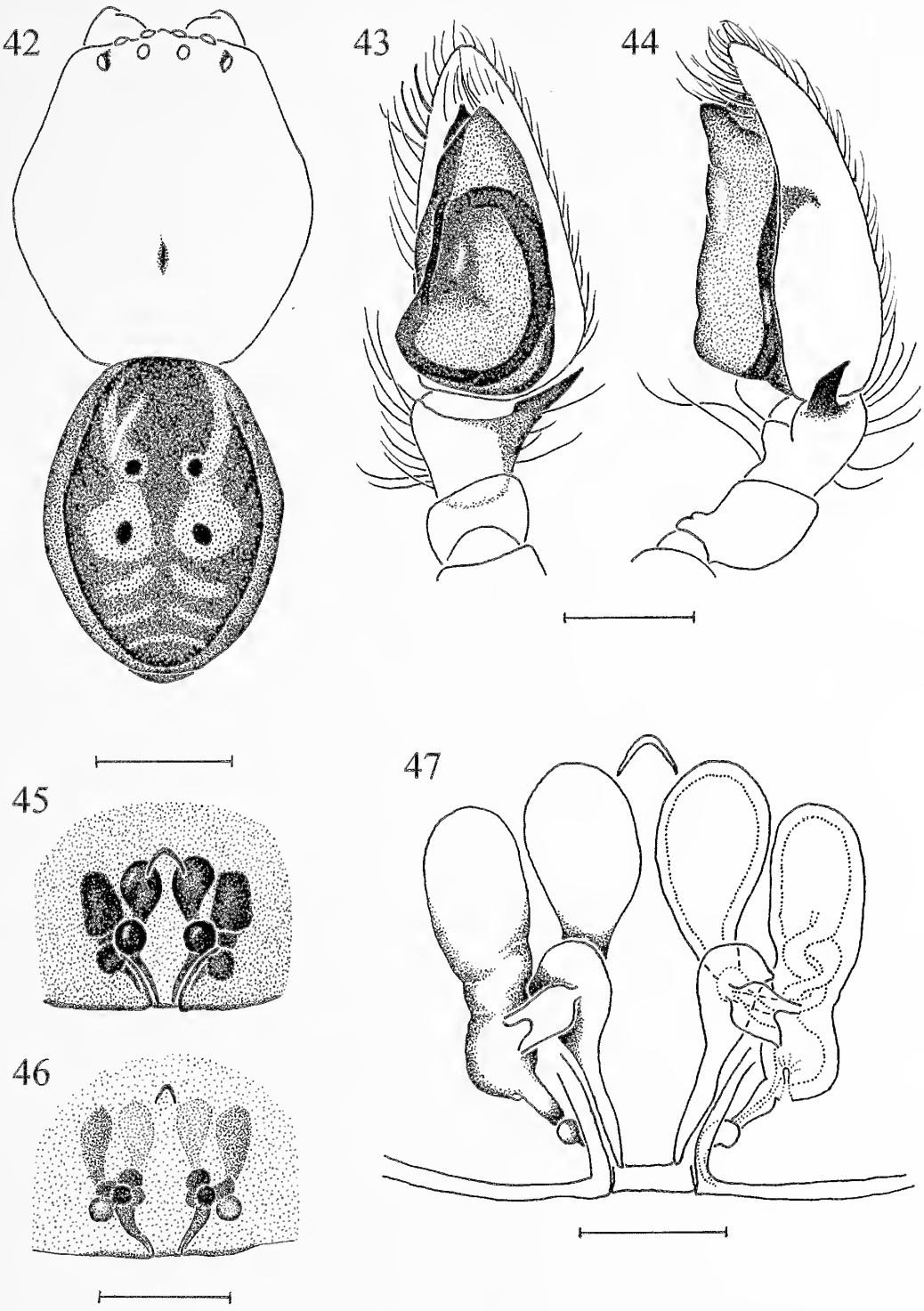
Epigynum poorly sclerotized, with a wide central depression anteriorly bordered by a broad, arc-shaped hood situated well in front of the large, piriform ST2 which are clearly visible through the transparent cuticle (Fig. 40). The large, oval COs are situated in the posterior part of the epigynal depression.

Distribution.—Black Sea region, Eastern Europe (Platnick 2008), Hungary, Croatia, Italy (Trotta 2005), France, Spain (Mallorca).

Remarks.—*Trachelas flavipes* Koch 1882 is only known from a single female from Sóller (Mallorca, Spain). In spite of collecting efforts, it has never been collected again on Mallorca (Pons & Palmer 1996). The type specimen has been lost (Braun 1965), but Koch's description (Koch 1882) is fully compatible with all characteristics of *T. maculatus*, a species which has been reported from Italy (Trotta 2005) and recently from France (Hervé, pers. comm.). Koch's poor drawings of the epigynum are surprisingly similar to the main outlines of ST2 and the large CO in the epigynal depression of *T. maculatus*, as also depicted in Chyzer & Kulczyński 1897:pl. 10 fig. 15c. *T. flavipes* is herewith synonymized with *T. maculatus*.

Trachelas validus Simon 1884
Figs. 5, 42–49

Trachelas validus Simon 1884:123.



Figures 42–47.—*Trachelas validus*: 42. Male, do; 43. Left male palp, ve; 44. Left male palp, rl; 45, 46. Epigyna, ve; 47. Vulva, ve. Scale bars: 42: 1 mm; 43–46: 0.25 mm; 47: 0.1 mm.

Types examined.—Holotype male, specimen in separate glass microtube, Spain, Burgos, Miranda de Ebro; paratypes: 2 males, 1 female, 2 juveniles, same data (MNHN-5659).

Other material examined.—SPAIN: *Salamanca*, Vallejera de Riofrío, (40°24′N, 5°44′W) 1200 m, oakwood, pt, 11 February 1984, 1♀, F. Ribas & C. Urones leg. (CCU). *Santander*, Puente Viesgo, (43°25′N, 3°97′W), 1 juv (MNCN). *Zamora*: Parque Regional del Lago de Sanabria, Cobreros (42°4′N, 6°42′W) oakwood, 1200 m, 11 April 2004, hc, 1♀ (JMA); 1300–1500 m, 12 September 2004, 1♂,1♀, subadult ♂♀ (JMA); 1100–1200 m, 11 October 2004, 2♀ (JMA); 1200–1350 m, 7 December 2004, 2♀ (JMA). Galende (42°6′N, 6°40′W) oakwood, 1400 m, 14 April 2004, hc, 1♀ (JMA); 1050 m, 15 April 2004, 2♀ (JMA); 1450 m, 7 August 2004, 1♀ (JMA); 1250 m, 12 October 2004, 1♀ (JMA); 1150 m, 5 December 2004, 1♀ (JMA). *León*, Villanueva de las Manzanas, under stones, hc, 12

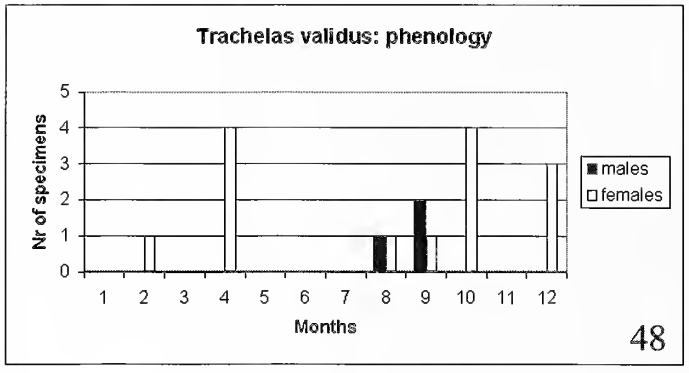


Figure 48.—*Trachelas validus*. Phenology.

August 1994, 1♂ (CRB). PORTUGAL: *Estremadura*: Tapada Nacional de Mafra (38°98′N, 9°35′W) Povoa de Cima, oakwood, 4 September 2001, pt, 1♂, G. Telfer leg. (CCU). Vila Pouca, pine wood, 1 October 2001, pt, 1♀, G. Telfer leg. (CCU). *Porto*, Porto, 2♂ (MNHN-19688).

Diagnosis.—*Trachelas validus* is closest to *T. ibericus*, from which it differs by its pitted sternum, by its male abdominal pattern consisting of a grey background with four large lighter patches surrounding the sigilla in the anterior half and a number of wide transversal light chevrons in the posterior half (Fig. 42), by the very short and blunt terminal embolus and the long and pointed, dorsally recurved RTA of the male palp (Figs. 43, 44), and by the narrow anterior hood of the epigynum (Figs. 45, 46).

Description.—*Male:* Total length 2.79–4.68 (HT 4.68, PT 3.36, 4.52). Carapace l 2.50, w 2.05, reddish brown to chestnut brown, covered with small pits carrying diminutive, transparent hairs. Cephalic part wide (3/4 of carapace width), rounded and bulging. Chilum single, sclerotized, brown.

Eyes subequal, anteriors separated by slightly less than one diameter, posteriors separated by about two diameters (Fig. 42). Clypeus height slightly larger than diameter of AME.

Chelicerae chestnut brown, rugose. Basal cheliceral boss very pronounced: anterior base of chelicerae protruding almost horizontally. Promarginal rim with three teeth, smallest one closest to cheliceral base (furthest from fang insertion), largest one in the middle. Retromarginal cheliceral rim with three teeth, diminishing in size towards fang base.

Sternum dotted with pits each carrying a pointed brown hair, orange brown with a darker border. PCT and ICS strongly sclerotized, blunt. PSP subtriangular. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II orange brown, legs III and IV orange yellow. Leg I with two rows of leg cusps (Platnick & Shadab 1974a; Platnick & Ewing 1995) on ti (pl 8–9, rl 1–2), mt (pl 7–10, rl 0–2), and ta (pl 3–4, rl 1–2), leg II with a single pl row of leg cusps on ti (4), mt (7–8), and ta (3). No ventral scopulae on ta, mt, and ti I and II. Leg formula 1,2,4,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	1.68	0.71	1.39	0.84	0.63	5.26
II	1.53	0.66	1.32	0.84	0.63	4.97
III	1.00	0.53	0.74	0.89	0.42	3.58
IV	1.32	0.58	1.13	1.32	0.50	4.84

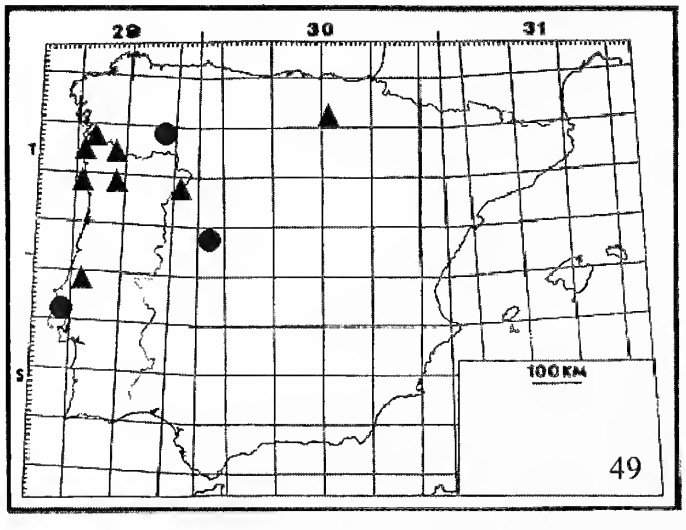


Figure 49.—*Trachelas validus*. Distribution on the Iberian Peninsula. Triangles: bibliographic data. Circles: new finds.

Abdomen grey with a brown dorsal scutum covering almost the entire abdomen and four light patches surrounding sigilla in anterior half, as well as a few wide, transversal light chevrons in posterior half (Fig. 42). Epigastric region sclerotized, yellow brown.

Male palp with a broad, long and sharp, dorsally recurved RTA (Fig. 44). Bulbus subtriangular, ending in a blunt tip which is situated retrolaterally of the short and blunt apical embolus. Sperm ducts partly discernable through transparent cuticle (Figs. 43, 44).

Female: Total length 4.52–4.89 (PT 4.52). Carapace l 1.97, w 1.66, reddish brown, covered with small pits carrying diminutive, transparent hairs. Cephalic part wide (3/4 of carapace width), rounded and bulging. Chilum single, sclerotized, brown.

All eyes subequal, except AME which are about 4/5 of others. Eyes in AER equidistant, separated by about 3/4 of AME diameter, eyes in PER also equidistant, separated by about 1.5 AME diameters (Fig. 6). Clypeus height slightly larger than diameter of AME.

Chelicerae brown, structured and toothed as in male, but cheliceral boss somewhat less pronounced.

Sternum dotted with pits each carrying a pointed brown hair, yellow brown with a darker border. PCT, ICS, and PSP as in male. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II orange brown, legs III and IV orange. Leg cusps absent. Dense ventral scopulae consisting of pale erectile bristles on ta and mt I and II, scopulae on ti I and II sparse to absent. Leg formula 4,1,2,3.

Leg measurements:

	fe	pa	ti	mt	ta	total
I	1.47	0.66	1.16	0.82	0.60	4.71
II	1.45	0.63	1.13	0.74	0.63	4.58
III	0.92	0.53	0.76	0.79	0.42	3.42
IV	1.32	0.58	1.18	1.32	0.47	4.87

Abdomen grey with a dark grey longitudinal dagger-shaped mark and four light patches surrounding sigilla in anterior half, as well as a few wide, transversal light chevrons in posterior half (Fig. 6). Dorsal scutum absent.

Epigynum poorly sclerotized, with a narrow, anterior, subtriangular arc-shaped hood. Two dark brown, circular, sclerotized COs separated by two diameters are situated somewhat more than halfway between anterior and posterior limit of epigynum. Clearly visible through the transparent cuticle are two large, piriform ST2 situated immediately anterior to the CO, and two similarly shaped ST1 situated laterally and exterior to these (Figs. 45, 46).

Vulva (Fig. 47) shows two large piriform ST2 posterior to a narrow, arc-shaped epigynal hood. Immediately posterior to ST2 are the heavily sclerotized COs, connected by a short stretch of ID to both ST2 and ST1, the latter situated laterally to the outside of ST2. ST1 subcylindrical, with long axis directed longitudinally, consisting of two lumina interconnected by two solenoidal, intertwined canals. The smaller; globose, posterior lumen is connected to the thin, tapering FD, the larger, ovoidal, anterior one communicates with the ID.

Natural history.—Ground-dwelling spider that has been collected in humus, leaf litter, *Buxus sempervirens* shrub (Simon 1884), on mosses, on walls (Machado 1937) and under stones, both as hand captures and in pitfalls. Lives in areas with diverse vegetation: Mediterranean Cork Oak wood (*Quercus suber* L.), Rebollo Oak wood (*Quercus pyrenaica* Willd.), Maritime Pine wood (*Pinus pinaster* L.) and riverine bush (with *Salix* sp.). Occurs over a large elevation gradient, from 10 m above sea level (Beira Litoral, Cardoso 2007) to 1500 m in the regions of Sanabria in Zamora. Adult males are found in August (Simon 1884) and September, adult females from August to December, as well as in February and April (Fig. 48).

Distribution.—An Iberian endemic (Melic 2001): has been cited from Spain, *Burgos* (Simon 1884) and Portugal (Simon 1898; Machado 1937; Cardoso 2004, 2007). Our data establish the presence of *T. validus* in the Spanish provinces León, Salamanca, Santander and Zamora (Fig. 49). They constitute the known Southern, Northern, and Western limits of distribution.

Remarks.—*Trachelas validus* is variable in genitalic morphology as well as in size. The transparency of the epigynum as well as the width of the anterior hood are variable (Figs. 45, 46). There is also variation in the length and dorsal curvature of the male palpal RTA and in the sharpness of the bulbus tip. Bosmans collected a quite small male specimen (body length 2.79) in Villanueva de las Manzanas.

Trachelas ibericus new species
Figs. 1–3, 50–57

Types examined.—Holotype male, Spain, Salamanca, Aldearrubia, (41°2′N, 5°28′W) 820 m, pine wood, pt, 9 October 1984, J.L. Fernández & C. Urones leg. (MNCN); allotype female: same data (MNCN); paratypes: 1 male, 1 female, Salamanca, Martinamor (Cuatro Calzadas) (40°49′N, 5°38′W) 900 m, Holm Oak wood, pt, 8 September 1984, J.L. Fernández & C. Urones leg. (CCU).

Other material examined.—SPAIN: *Córdoba*, Arroyo Calderas (37°54′N, 5°12′W) 183 m, pt, 4 January 1983, 1♀, M. Gaju leg. (CCU). *Gerona*, Fitor, (41°54′54″N, 3°5′25″E) 230 m, *Eucalyptus* plantation, sl, 6 August 2002, 1♂, J. Bosselaers leg. (CJB). *Salamanca*, Aldearrubia, (41°2′N, 5°28′W) 820 m, pine wood, pt, 2 February 1984, 1♀, F. Ribas & C. Urones leg. (CCU); 22 March 1984, 1♀, F. Ribas & C. Urones leg. (CJB); 23 April 1985, 1♀, J.L. Fernández & C. Urones leg. (CCU). Béjar (40°22′N, 5°47′W) 900 m, Chestnut wood, pt, 8 September 1984, 1♂, M. Jerardino & C. Urones leg. (CCU); 25 September 1984, 1♂, M. Jerardino & C. Urones leg. (CCU); 30 October 1984, 1♂, M. Jerardino & C. Urones leg. (CCU). Martinamor (Cuatro Calzadas) (40°49′N, 5°38′W) 900 m, Holm Oak wood, pt, 31 March 1984, 4♀♀, F. Ribas & C. Urones leg. (CCU); 5 May 1984, 1♀, F. Ribas & C. Urones leg. (CCU); 26 June 84, 1♀, F. Ribas & C. Urones leg. (CCU); 25 August 1984, 1♂, J.L. Fernández & C. Urones leg. (CCU); 25 September 1984, 2♂♂, J.L. Fernández & C. Urones leg. (CCU); 9 October 1984, 1♂, J.L. Fernández & C. Urones leg. (CCU); 6 December 1984, 2♂♂1♀, J.L. Fernández & C. Urones leg. (CJB, CCU); 28 March 1985, 2♀♀, J.L. Fernández & C. Urones leg. (CJB, CCU). *Cáceres*, Talavan, Finca Del Baldio, pt, 10 July - 8 November 1996, 1♂, U. Stengele leg. (CRB). PORTUGAL, *Alto Alentejo*, Évora, Montemor-O-Novo, Autumn 2004, 1♂, S. Mendes leg. (no further data). FRANCE, *Pyrenées Orientales*, Banyuls, 4 November 1911, 1♀, (misidentified as *T. rayi*) (MNHN-4.25.9.62, Collection Berland). ALGERIA, *Oran*, Daya, 1♀ (misidentified as *T. amabilis*) (MNHN1874)

Etymology.—The species epithet *ibericus* refers to the Iberian Peninsula, where almost all specimens were collected.

Diagnosis.—*Trachelas ibericus* is closest to *T. validus*, from which it differs by its yellow-brown overall color, smooth sternum and lack of male abdominal pattern, by the very small, pointed RTA, by the male bulbus having a conspicuous basal bump and a long and pointed, prolaterally curved embolus adjacent to a transparent, flat, membranaceous conductor (Figs. 51, 52), and by the sclerotized epigynum with conspicuous anterior COs and a median longitudinal crest in females (Figs. 53, 54).

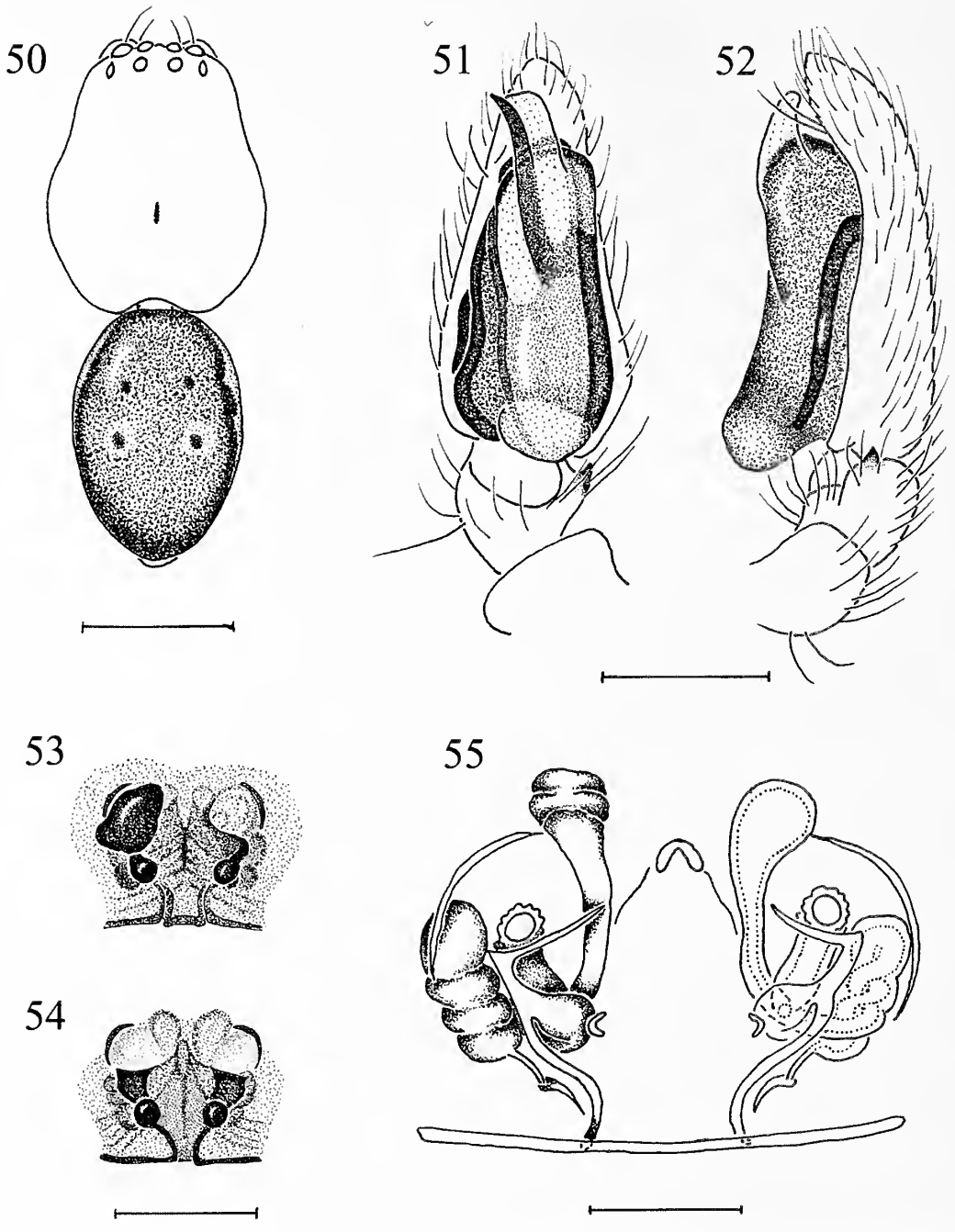
Description.—*Male:* Total length 2.65–3.47. Carapace l 1.74, w 1.47, yellow-brown, covered with small pits carrying diminutive, transparent hairs. Cephalic part wide (slightly less than 3/4 of carapace width), rounded and bulging. Chilum single, sclerotized, yellow-brown (Fig. 1).

Eyes subequal, anteriors separated by about 1/2 diameter, posteriors separated by about 1.5 diameters (Fig. 50). Clypeus height slightly smaller than diameter of AME.

Chelicerae yellow-brown, rugose. Basal cheliceral boss very pronounced: anterior base of chelicerae protruding almost horizontally (Fig. 2). Promarginal rim with three teeth, smallest one closest to cheliceral base (furthest from fang insertion), largest one in the middle. Retromarginal cheliceral rim with three teeth, diminishing in size towards fang base.

Sternum almost smooth, yellow-brown with a darker border. PCT and ICS blunt, PCT only weakly sclerotized. PSP subtriangular. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II brown, legs III and IV yellow-brown. Tibiae I and II with one pl row of leg cusps (I 8–13, II 7–10), two rows of leg cusps on mt (I pl 6–8, rl 2–4; II pl 5–6, rl 0–2) and ta (I pl 4–5, rl 2–3; II pl 3–4, rl



Figures 50–55.—*Trachelas ibericus* new species: 50. Male, do; 51. Left male palp, ve; 52. Left male palp, rl; 53, 54. Epigyna, ve; 55. Vulva, ve. Scale bars: 50: 1 mm; 51–54: 0.25 mm; 55: 0.1 mm.

0–2) (Fig. 3). No ventral scopulae on ta, mt and ti I and II. Leg formula 1,2,4,3.

Leg measurements:

	Fe	pa	ti	mt	ta	total
I	1.21	0.45	0.97	0.63	0.53	3.79
II	1.03	0.42	0.92	0.63	0.50	3.50
III	0.71	0.34	0.60	0.66	0.32	2.63
IV	0.87	0.39	0.79	0.89	0.42	3.37

Abdomen grey, without pattern and with a yellow-brown dorsal scutum covering almost the entire abdomen (Fig. 50). Epigastric region sclerotized, yellow brown.

Male palp with an inconspicuous, pointed, very small RTA (Fig. 52). Bulbus subtriangular, with a protruding basal bump (Fig. 52). Embolus long and pointed, prolaterally curved, inserted in anterior half of bulbus and adjacent to a transparent, flat, membranaceous conductor (Fig. 51). Sperm ducts partly discernable through transparent cuticle (Figs. 51, 52).

Female: Total length 3.81–4.05. Carapace l 1.58, w 1.28, Yellow-brown, covered with small pits carrying diminutive, transparent hairs. Cephalic part wide (slightly less than 3/4 of carapace width), rounded and bulging. Chilum single, sclerotized, brown.

All eyes subequal, anteriors separated by less than one diameter, AME closer to each other than to ALE. Posterior

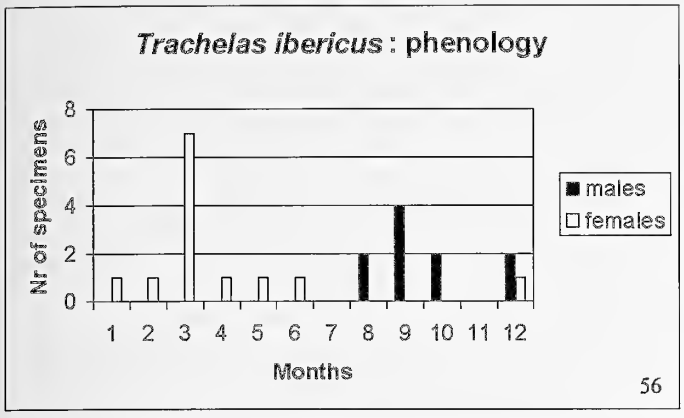


Figure 56.—*Trachelas ibericus*. Phenology.

eyes equidistant, separated by about 1.5 diameters (Fig. 7). Clypeus height slightly smaller than diameter of AME.

Chelicerae colored, structured and toothed as in male, but cheliceral boss somewhat less pronounced.

Sternum dotted with pits each carrying a pointed brown hair, yellow-brown with a darker border. PCT, ICS, and PSP as in male. Labium as long as wide. Maxillae without oblique depression.

Legs spineless, covered with fine hairs, legs I and II orange-yellow, legs III and IV yellow. Leg cusps absent. Dense ventral scopulae consisting of pale erectile bristles on ta, mt, and ti I and II. Leg formula 4,1,2,3.

Leg measurements:

	Fe	pa	ti	mt	ta	total
I	1.05	0.39	0.84	0.60	0.50	3.39
II	1.00	0.39	0.84	0.60	0.47	3.31
III	0.76	0.34	0.55	0.58	0.34	2.58
IV	1.05	0.42	0.89	0.97	0.39	3.73

Abdomen grey with a dark grey longitudinal dagger-shaped mark flanked by two large, crescent shaped longitudinal light spots anteriorly, followed by two transversal median light patches and a number of thin transversal chevrons in posterior part (Fig. 7). Dorsal scutum absent.

Epigynum sclerotized, anterior hood inconspicuous and subtriangular. Symmetry axis of epigynum with a pronounced, longitudinal median crest (Figs. 53, 54). Two large COs in anterior half, often plugged by a dark brown secretion (Fig. 53).

Vulva (Fig. 55) shows two narrow and elongated, median ST2 flanked laterally by a longitudinally elongated ST1 consisting of two small lumina interconnected through two solenoidally coiled, intertwined canals.

Natural history.—Lives in the Mediterranean climate zone, in semi-arid regions with dry and hot summers and cold winters, as well as in humid regions with high precipitation in winter. Has been found such diverse vegetation types as evergreen Holm Oak wood (*Quercus ilex* ssp. *ballota* (Desf.) Samp.), Italian Stone Pine wood (*Pinus pinea* L.), and deciduous Chestnut wood (*Castanea sativa* Miller). Large altitude range: 180–900 m. Specimens have been collected in pitfalls and by hand capture or sifting litter. Adult females

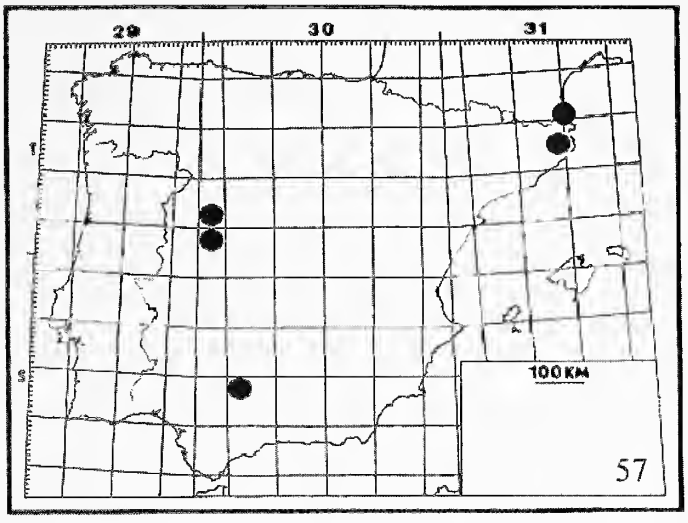


Figure 57.—*Trachelas ibericus*. Distribution on the Iberian Peninsula and in France.

were captured during most of the year, being most frequent in March and absent in Fall. Adult males appear in the second half of the year, being most frequent from August to October (Fig. 56).

Data on the biology of the species are scarce: the animals prefer humus and litter, often looking for shelter behind bark or under stones. The species builds no web, but constructs a silk retreat where the female guards its egg sac.

Distribution.—Recorded from the Western Mediterranean: the northeast, west and south of Spain (Fig. 57), as well as southeast France and northwest Algeria.

Remarks.—The specimens attributed by de Jerardino et al. (1991) and Urones et al. (1990) to a "species close to *Trachelas minor*?" belong to the present species. The citation of *Cetonana laticeps* by Urones et al. (1985) is an error and in reality concerns *T. ibericus* as well.

Cetonana laticeps (Canestrini 1868)

Material examined.—SPAIN: *Gerona*, Bañolas, Pujals dels Caballers, DG86, 1 November 1982, 1♂, J.A. Pérez leg. (CCU).

Diagnosis.—*Cetonana laticeps* differs from the Mediterranean *Trachelas* species by the presence of well sclerotized, sharper, and more pronounced PCT; leg cusps that are present on mt and ta of legs I and II in males as well as females; a flat carapace; AME that are cleary larger than the other eyes; scopulae of erectile bristles in females, which are restricted to ta and basal part of mt I and II; a female epigynum with posterior CO's; and a male palp with a bulbus occupying only part of the ventral side of the cymbium (Grimm & Vilbel 1986). In contrast, the Mediterranean *Trachelas* species have small and often weakly sclerotized PCT; leg cusps on ti, mt and ta of legs I and II, which are present in males only (and only in some species); a carapace that bulges in the cephalic region; subequal eyes; females with dense ventral scopulae consisting of pale erectile bristles on ta, mt and ti I and II; a female epigynum with median or anterior Cos; and a male palpal bulbus occupying the entire ventral side of the cymbium.

Remarks.—The present citation is the only known record of this species for the Iberian Peninsula. As stated above, the citation of *Cetonana laticeps* by Urones et al. (1985) was an error.

DISCUSSION

Most of the old world *Trachelas* species are rare, have a hidden lifestyle and, contrary to a number of new world species who have been reported as inflicting bites to humans (Platnick & Shadab 1974a; Pase 1978), never occur close to houses. As a result, they are seldom collected and, to date, most species were considered to have a limited or even endemic distribution area. The present revision considerably alters this perception. *Trachelas minor* was already known as widespread, occurring from Azerbaijan to West Africa. *Trachelas canariensis*, on the other hand, was considered a Canarian endemic. It is now found to be a widespread species, recorded from equatorial Africa to Spain. Another former Canarian endemic, *T. macrochelis*, is reported in the present study from Algeria and mainland Spain as well. *Trachelas rayi*, mentioned from France and Italy in Platnick (2008), is also reported here from Spain and Algeria, while *T. maculatus*, called a "Black Sea species" by Mikhailov (1987), in reality has a distribution area reaching from Eastern Europe to France and Spain. The only two species that were not found outside their known distribution areas are the northwest African *T. amabilis* and the Iberian endemic *T. validus*. Although apparently considerably more widespread than previously thought, the old world *Trachelas* species avoid Northern latitudes: none of the 16 species mentioned above have been collected North of 50° of latitude. As a matter of fact, the epicentre of the distribution of the eight *Trachelas* species presently known from the Mediterranean is the Iberian Peninsula. In this region, the distribution areas of the widespread *T. minor, T. maculatus*, and *T. canariensis* overlap with those of the Western Mediterranean *T. rayi, T. macrochelis*, *T. ibericus*, and *T. validus*. The North African *T. amabilis* is the only Mediterranean *Trachelas* which has not yet been collected from the Iberian Peninsula.

Simon (1897: 180) already noted that *Trachelas* is not a very homogenous genus: "Ce genre est fort nombreux et peu homogène, au point qu' on serait tenté de le fractionner si l'on ne tenait compte de tous les intermédiaires gradués qui relient ses formes extrèmes." Morphologically, the Mediterranean *Trachelas* species can be divided into three groups.

The *minor* group is characterized by the absence of a chilum, median eyes further removed from each other than from laterals, maxillae with a shallow oblique transversal depression, male palpal femur with ventral terminal groove, male palpal patella with retrolateral apophysis, absence of RTA, an inflated, pear-shaped bulbus, globular ST1 and ST2 connected to the anteriorly positioned COs by thin, anteriorly coiled ducts. Apart from *T. minor* and *T. canariensis*, the *minor* group encompasses the Afrotropical species *T. pusillus, T. chubbi*, and *T. sylvae*, and most probably also the east Palearctic species *T. alticolus, T. japonicus*, and *T. sinensis* and the Oriental species *T. himalayensis* Biswas 1993, *T. oreophilus* Simon 1906, and *T. quisquiliarum* Simon 1906. *Trachelas costatus* was considered close to *T. maculatus* by Mikhailov (1987: 1586). However, O. Pickard-Cambridge's drawing (1885:Pl. II, fig. 21d) clearly suggests that this species belongs in the *minor* group. The *minor* group further encompasses a number of newly discovered African species (Lyle 2008).

The *rayi* group is characterized by a very broad cephalic part of the carapace in males, a blunt RTA, an oval bulbus with a short apical embolus, a poorly sclerotized epigynum with a medially situated, wide epigynal hood, large anterior piriform ST2, and ST1 consisting of two globular, interconnected lumina. *Trachelas rayi, T. amabilis*, and *T. macrochelis* belong to this group.

The *validus* group is characterized by the presence of leg cusps on at least ti and mt of leg I in males, male legs I and II which are stout and longer than leg IV, a pear-shaped bulbus, an anteriorly situated epigynal hood, and longitudinally oriented lateral ST1 consisting of two lumina interconnected by solenoidally coiled canals. Apart from *T. validus, T. maculatus*, and *T. ibericus*, the Oriental species *T. acuminus* and *T. coreanus* also belong in this group (but see Kim & Lee 2008).

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A new micro-whip scorpion species from Brazilian Amazonia (Arachnida, Schizomida, Hubbardiidae), with the description of a new synapomorphy for Uropygi

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Abstract. *Surazomus uarini* n. sp. is described and illustrated based on specimens collected by beating on understory vegetation of Amazonian "terra firme" upland rain forests. A new cuticular structure, possibly a gland opening, is described on the female tarsus I and terminal flagellum. A putatively homologous structure is reported from the same body parts in an undescribed species of *Rowlandius* Reddell and Cokendolpher 1995; *Stenochrus portoricensis* Chamberlin 1922; *Mastigoproctus maximus* (Tarnani 1889); and *Thelyphonellus amazonicus* (Butler 1872); suggesting a new synapomorphy for the clade Uropygi (i.e., Schizomida + Thelyphonida).

Keywords: *Surazomus uarini*, *Rowlandius*, *Stenochrus*, *Mastigoproctus*, *Thelyphonellus*, gland opening, Neotropical, taxonomy

The schizomid fauna of Brazil is relatively poorly known. Currently, only nine species have been recorded for the country (Harvey 2003; Bonaldo & Pinto-da-Rocha 2007), one of them introduced into the Rio de Janeiro coast (Tourinho & Kury 1999) and the remaining species restricted to Amazon forest localities (Cokendolpher & Reddell 2000; Reddell & Cokendolpher 2002). Most of the Brazilian species have been described over the last 10 years as a result of the growing use of collecting methods designed to sample small, ground-dwelling arthropods in different sites of the Amazonian rain forest. The majority of Brazilian schizomid species are known from several specimens recorded only in their type-localities or vicinities. Since the leaf-litter sampling available so far are mainly from Central Brazilian Amazonia, especially in the vicinities of the city of Manaus, and schizomid species are usually endemic to narrow areas, we expect that several new species from Amazonia are waiting to be discovered and described. In this study, a new species of hubbardiid micro-whip scorpion is described and illustrated based on a few specimens collected in western Amazonia. In contrast to other species of the order, *Surazomus uarini* n. sp. was collected from understory vegetation, not leaf-litter. The description also includes a short note on a peculiar cuticular structure, supposedly a gland opening, discovered during SEM study.

METHODS

The material examined is lodged in the following collections (abbreviations and curators in parenthesis): Fundação Universidade do Amazonas, Manaus (UA, N.O. Aguiar); Instituto Butantan, São Paulo (IBSP, A.D. Brescovit); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA, A. Henriques); Museu de Zoologia, Universidade de São Paulo (MZSP, R. Pinto-da-Rocha). The specimens were examined and illustrated while immersed in 70% ethanol, under a Leica MZ12.5 stereomicroscope with a camera lucida. In order to examine internal female genitalia, the first opisthosomal sternite was excised, provisionally mounted on a microscope slide with clove oil and illustrated using a Zeiss Axioscope 2 Plus binocular microscope with a camera lucida. The appendages examined under a scanning electron microscope (SEM) were removed from specimens, air dried, and fixed on stubs with double-sided tape. The stubs were sputter-coated with gold and then examined with a JEOL (JSM 840A) SEM microscope at the Laboratório de Microscopia Eletrônica, Insituto de Física, USP. The description format follows Pinto-da-Rocha (1996), cheliceral setae were grouped according to Reddell & Cockendolpher (1995:fig. 14). All measurements are in mm.

Additional material examined.—*Rowlandius* new species: BRAZIL: *Paraíba*: 1 ♀, João Pessoa, Área de Proteção Permanente Mata do Buraquinho (07°06′S, 34°52′W), 14–22 October 2003, S.C. Dias (IBSP 003).

Stenochrus portoricensis: BRAZIL: *Bahia*: 1 ♀, Ilhéus, Campus CEPLAC (14°45′16″S, 39°13′50″W), 27 February–6 September 2007, P.P. Santos (IBSP 24).

Mastigoproctus maximus: BRAZIL: *Mato Grosso*: 1 ♀, Chapada dos Guimarães, Usina Hidrelétrica de Manso, 2000, equipe Resgate de Fauna (IBSP 240).

Thelyphonellus amazonicus: BRAZIL: *Amapá*: 1 ♀, Serra do Navio, C.Froelich, W. Narchi (MZSP 14319).

Family Hubbardiidae Cook 1899
Genus *Surazomus* Reddell & Cokendolpher 1995

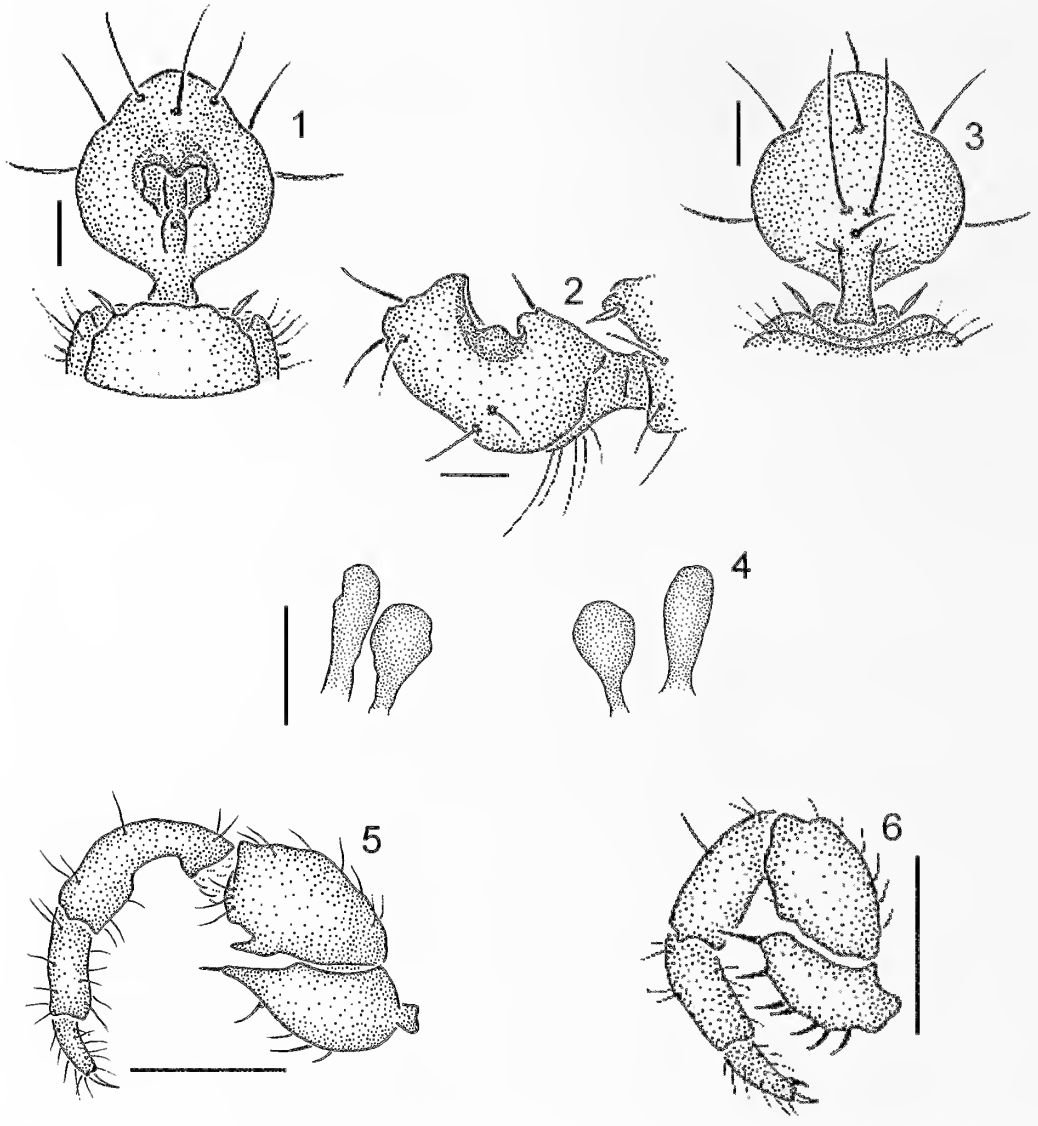
Surazomus Reddell & Cokendolpher 1995:116–117.

Type species.—*Trithyreus sturmi* Kraus 1957, by original designation.

Remarks.—The genus *Surazomus* currently comprises thirteen species, distributed in Costa Rica and northern South America (Harvey 2003; Bonaldo & Pinto-da-Rocha 2007). Most species occur in the Amazonian forest, mainly in Brazil (six species), Colombia (three species), Ecuador, Peru, and Bolivia (one species each). The new species described below is the seventh known species from Brazilian Amazonia.

Surazomus uarini new species
(Figs. 1–14)

Material examined.—BRAZIL: *Amazonas*: holotype male, Uarini, 03°02′57″S, 65°41′42″W, 22 July–3 August 1995, P.F.



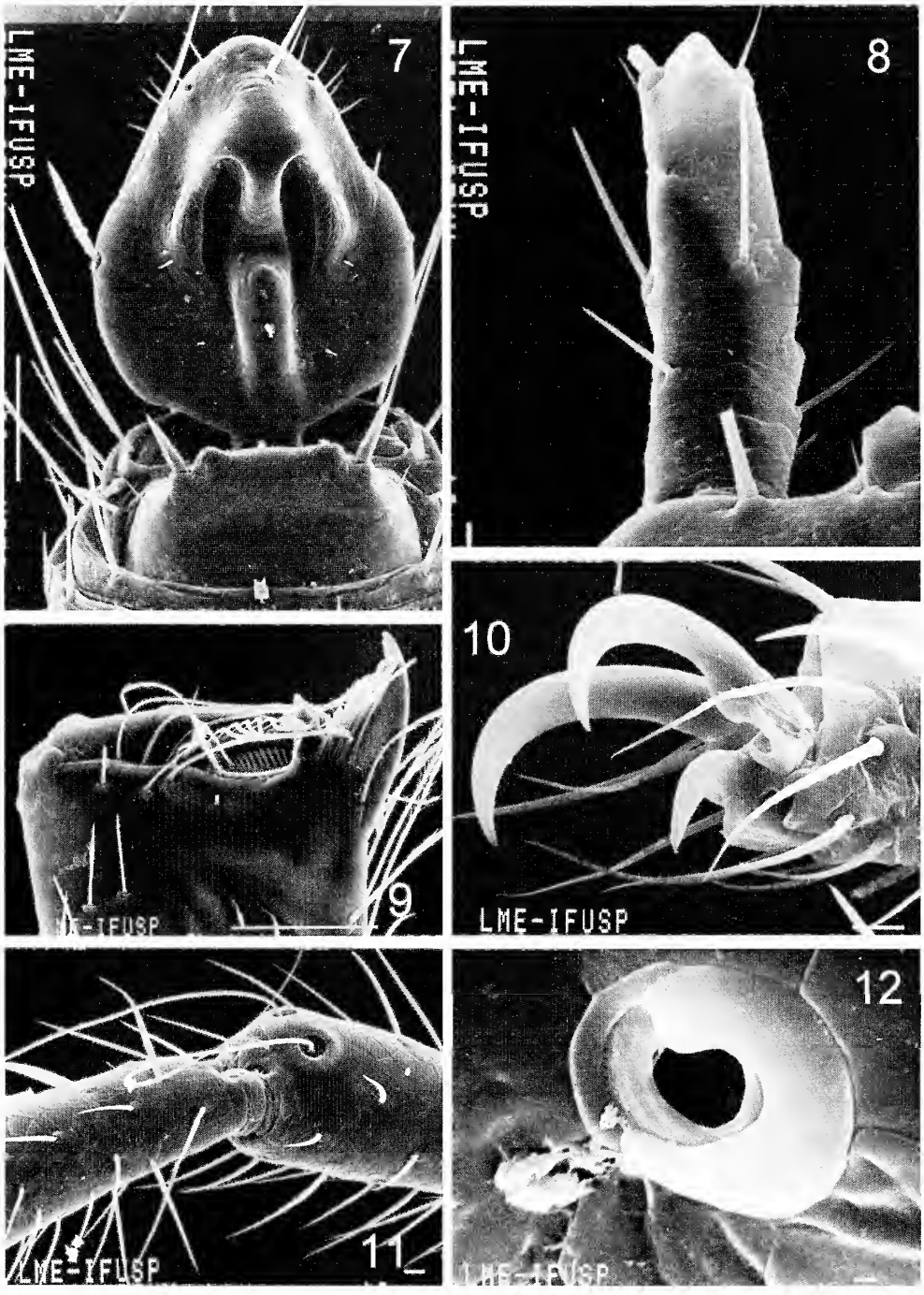
Figures 1–6.—*Surazomus uarini* new species: 1. Male flagellum, dorsal view; 2. Same, lateral view; 3. Same, ventral view; 4. Female internal genitalia, dorsal view; 5. Left male pedipalpus, retrolateral view; 6. Left female pedipalpus, retrolateral view. Scale lines = 0.1 mm (Figs. 1–3), 0.05 mm (Fig. 4), 0.5 mm (Figs. 5, 6).

Bührnheim, N.O. Aguiar (UA). Paratypes: 1 female, collected with holotype (UA); 2 males, 2 females, 2 juveniles, Coari, Rio Urucu, near the airport (04°53′05″S, 65°22′09″W), 17–23 February 1996, P.F. Bührnheim, N.O. Aguiar (IBSP 001); 1 male, 1 female, same data (INPA); 2 males, 2 females, 2 juveniles, same data (UA); 1 male, 1 female, 2 juveniles, same data except 26–29 April 1996 (MZSP 28375).

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—*Surazomus uarini* is similar to *S. rodriguesi* Cokendolpher & Reddell 2000 and *S. mirim* Cokendolpher & Reddell 2000 by the absence of a dorso-apical apophysis on the penultimate segment of the flagellum (Fig. 8). It also shares with *S. rodriguesi* the presence of a pair of plumose setae (vl1) and a pair of hollow depressions on the dorsal surface of the male flagellum (Figs. 1, 7). These species can be distinguished by the normal vl2 setae (plumose in *S. rodriguesi*), hollow depressions in a median position (median-anteriorly positioned in *S. rodriguesi* and *S. mirim*), and the dorsal surface more pronounced posteriorly to the hollow depressions (dorsal surface flattened in *S. rodriguesi*) (Figs. 1–3, 7).

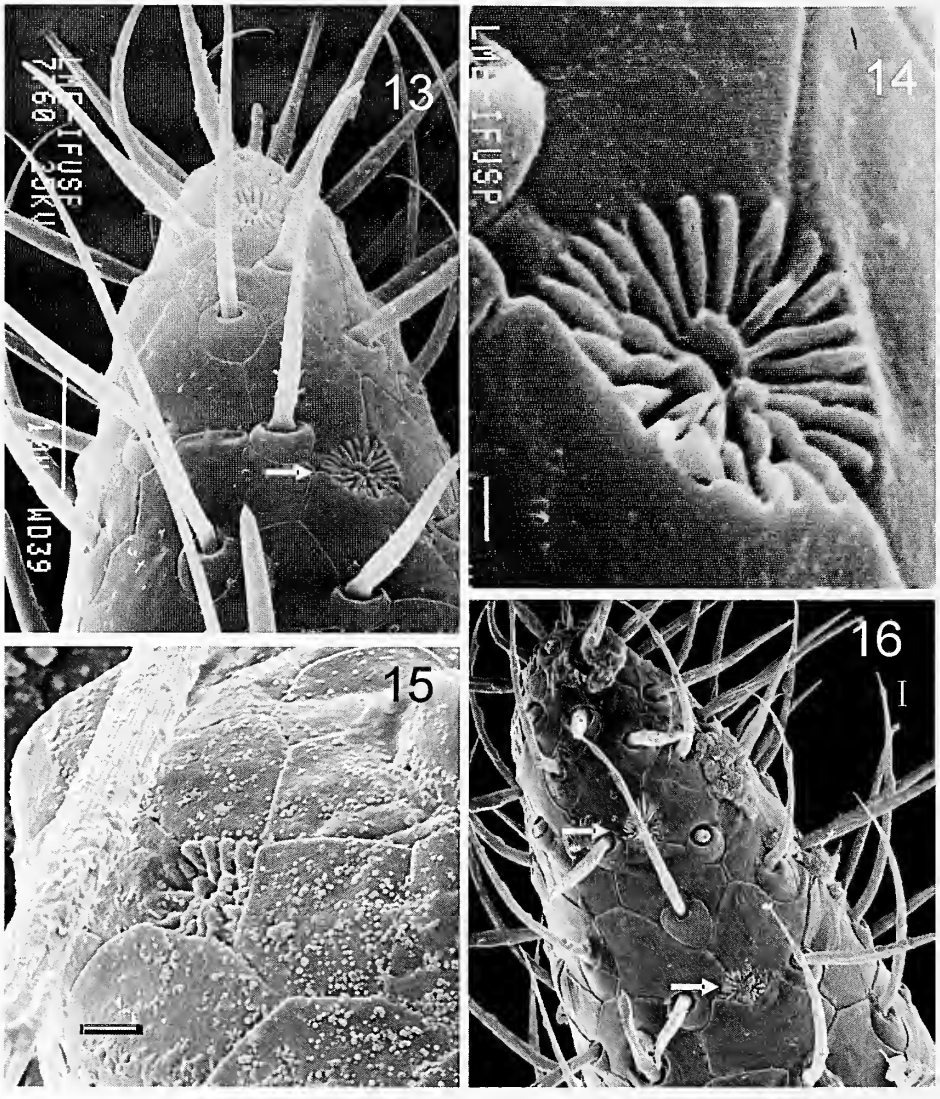
Description.—*Male (holotype)*: propeltidium, metapeltidium, and tergites brownish. Pedipalpus, chelicerae and legs brownish, patella I white in the apical third. Eye spots white and irregular. Propeltidium with three pairs of setae and two setae in a row on the anterior process. Metapeltidium narrowly divided. Anterior sternum with 12 setae, abdominal tergites with two setae each. Opisthosomal tergite XII with two lateral simple and two dorsal spatulate setae. Postero-dorsal process vestigial. Terminal flagellum slightly trilobate, with two median hollow depressions delimited laterally by a keel (Figs. 1–3). Flagellum with two lateral paired setae, three dorsal unpaired (Fig. 1), one paired and four unpaired (Fig. 3). Chelicerae (Fig. 9) fixed finger with three smaller denticles between two primary teeth. Serrula of movable finger with 11 teeth. Guard tooth absent, without accessory teeth. Number of setae in group 1 = 3, 2 = 3, 3 = 4, 4 = 2, 5 = 5,



Figures 7–12.—*Surazomus uarini* new species, scanning electron micrographs: 7. Male flagellum, dorsal view; 8. Female flagellum, dorsolateral view; 9. Male chelicerae, ventral view; 10. Male leg IV, tarsal claws; 11. Male tarsus I, penultimate segment, apical trichobothria; 12. Male pedipalpus, base of trichobothrium. Scale lines = 100 μm (Figs. 7, 9), 10 μm (Figs. 8, 10, 11), 1.0 μm (Fig. 12).

6 = 1. Trochanter of pedipalpus with strong acute apical spur and short mesal spur, femur with strong, curved and short (1/3 the length of femur) ventromesal spur (Fig. 5). Patellae curved and constricted in the first half. Penultimate segment of tarsus I with a pair of long dorsal trichobothria, each with a simple base (Fig. 11). Remaining leg trichobothria shorter and with sculptured bases (Fig. 12). Tarsal claws unarmed (Fig. 10), about 1/3 the tarsus length. Tarsal spur ~ 1/5 tarsus length. Total length (excluding flagellum) 2.7, carapace 1.1 long. Flagellum 0.35 long, 0.27 wide. Length of leg segments: I – Femur 0.77/patella 0.85/tibia 0.62/basitarsus-telotarsus 0.62; II – 0.57/0.25/0.35/0.65; III – 0.5/0.2/0.25/0.52; IV – 0.85/0.22/0.52/0.72. Basitarsus-telotarsus I segment lengths: 0.2/0.4/0.4/0.5/0.5/0.5/0.1.

Female (paratype, UA): color and body setation as in male. Flagellum three segmented. Internal genitalia with two lateral pairs of spemathecae. Ectal spermathecae finger-shaped, mesal ones oval, with short ducts (Fig. 4). Trochanter of pedipalpus with rounded apex, without spur (Fig. 6). Patella spur replaced by a short rounded projection. Total length 3.13,



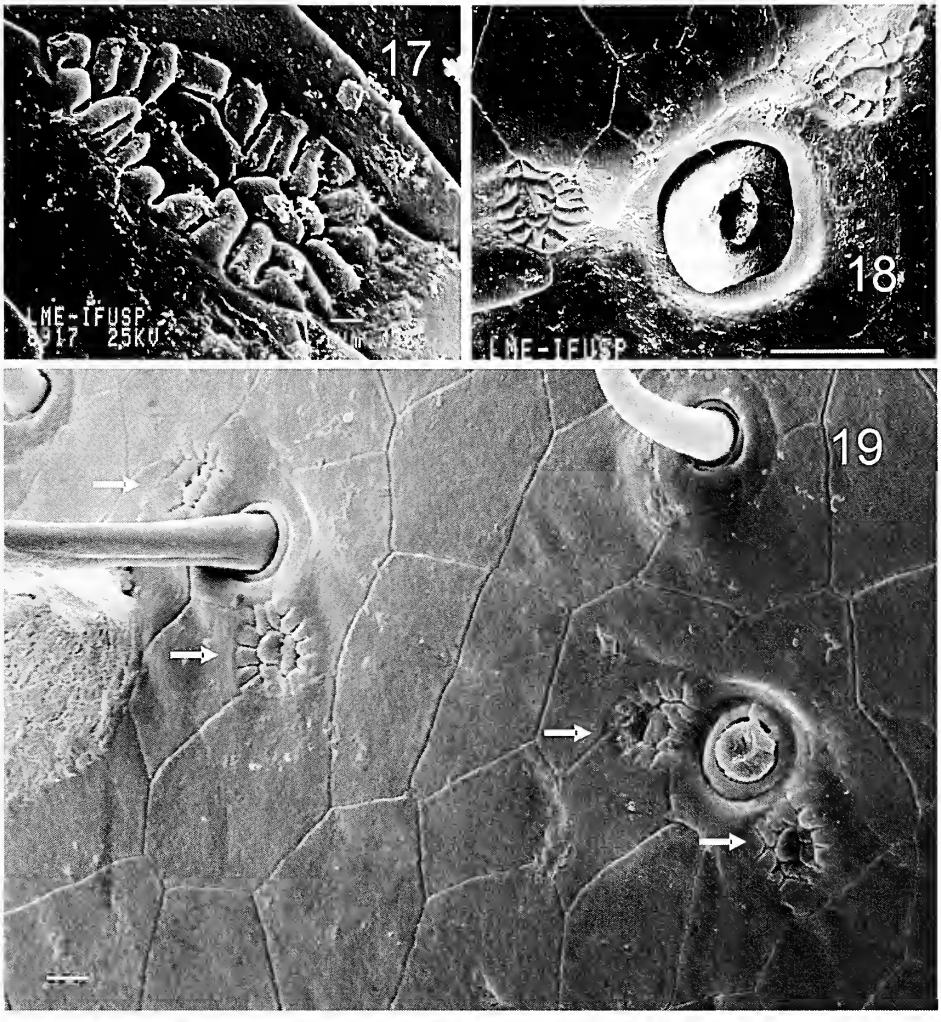
Figures 13–16.—Glandular openings of Schizomida. 13, 14. *Surazomus uarini* new species: 13. Female tarsus I, last segment (arrow: glandular opening); 14. Same, magnified; 15. *Rowlandius* new species, female flagellum, glandular opening; 16. *Stenochrus portoricensis* Chamberlin, 1922, female tarsus I (arrows: glandular openings). Scale lines = 10 μm (Fig. 13), 1.0 μm (Fig. 14), 3.0 μm (Figs. 15, 16).

carapace 1.25 long. Flagellum 0.2 long, 0.05 wide. Length of leg segments: I – femur 0.8/patella 0.95/ tibia 0.6/basitarsus 0.55; II – 0.62/0.32/0.35/0.6; III – 0.5/0.22/0.27/0.5; IV – 0.87/ 0.35/0.6/0.82. Basitarsus-telotarus segment lengths: 0.2/0.3/0.4/ 0.4/0.5/0.5/0.1.

Variation.—Carapace length, males: 0.95–1.1 (n = 6), females: 1.1–1.2 (n = 5). One of the male paratypes (INPA) has the pedipalpus similar to those of females, without spurs on trochanter and femur.

Natural history.—All specimens were collected by beating understory vegetation, mainly on Araceae and Palmae. Amazonian schizomids are usually found in litter or the superficial soil layer, although one species (*Surazomus arboreus* Cokendolpher & Reddell 2000) was observed climbing trees in seasonally flooded Amazonian forests (Cokendolpher & Reddell 2000). *Surazomus uarini* was collected only in non-flooded, upland "terra-firme" forest localities.

Gland opening.—A peculiar cuticular structure was observed in male and female sensorial tarsus I (Fig. 13) and the flagellum. It consists of an aperture with several grooves radiating from a central pore (Fig. 14), and is distributed over much of the segment (Fig. 13). This structure could be a sensory organ or a glandular opening. Several arachnid orders have pore-like chemosensory organs on the tarsus, including Amblypygi (Weygoldt 2000), Araneae (Foelix 1996), and Ricinulei (Talarico et al. 2005). Similar structures are also present in other arthropod groups, although they are usually simple, with only one aperture (see Hallberg & Hansson 1999). The shape of this structure is more consistent with an exocrine gland opening derived from the epidermis (see Noirot & Quennedy 1974, 1991); only histological studies using electron microscopy can fully elucidate its nature. To verify whether this presumed glandular opening is present in other genera of Schizomida and Thelyphonida, we examined other specimens by using a scanning electron microscope. Similar openings were found on tarsus I and flagellum of two other hubbardiid species: in the female of an undescribed species of *Rowlandius* Reddell & Cokendolpher 1995 from northeastern Brazil (Fig. 15), and in the female of *Stenochrus portoricensis*



Figures 17–19.—Glandular openings of Thelyphonida: 17, 18. *Mastigoproctus maximus* (Tarnani 1889): 17. Female tarsus I, glandular opening; 18. Female flagellum, glandular opening. 19. *Thelyphonellus amazonicus* (Butler, 1872): Female tarsus I (arrows: glandular openings). Scale lines = 1.0 μm (Fig. 17), 10 μm (Fig. 18), 3 μm (Fig. 19).

Chamberlin 1922 (Fig. 16). This structure was also observed in the tarsus I and flagellum of *Mastigoproctus maximus* (Tarnani 1889) (Figs. 17, 18) and *Thelyphonellus amazonicus* (Butler 1872) (Fig. 19). As far as we know, nothing similar to that has been reported in other arachnid orders, suggesting that these gland openings could be synapomorphic for the clade Uropygi (sensu Shultz 1990). This hypothesis can be tested in the future with a larger sample of schizomids and thelyphonids, as well as detailed comparisons with other arachnids. It is not impossible that this uropygid gland opening is homologous to the "pit organ" or the "plate organ," two sculptured pore-like structures commonly found in sensory first tarsi of amblypygids, also with unknown function (Weygoldt 2000). In that case, the Uropygi-synapomorphy hypothesis would depend on determining which shape of this structure is apomorphic.

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Revised diagnosis and redescription of *Apistobuthus susanae* (Scorpiones, Buthidae)

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Abstract. The scorpion *Apistobuthus susanae* Lourenço 1998 is redescribed based on new specimens collected from Khoozestan Province, Iran. It is distinct from *A. pterygocercus* Finnegan 1932 found in the dunes of Rub' al-Khali. The two species cannot be separated by previously used diagnostic characters. Instead, *A. susanae* is differentiated from *A. pterygocercus* by new characters, including more robust legs and pedipalps, shorter pectines, stronger carination, and complete fusion of central lateral and posterior median carinae of the carapace.

Keywords: Taxonomy, scorpion, Iran, Arabia

In 1932, Dr. Susan Finnegan at the British Museum of Natural History studied three specimens of a remarkable new buthid scorpion collected by the British explorer Sir Bertram Thomas in 1930, on his camel voyage across the vast sand sea of southern Arabia, the Rub' al-Khali or Empty Quarter (Thomas 1931, 1932). She assigned this scorpion to a new genus and species, *Apistobuthus pterygocercus* or "incredible buthid with winged tail," a reference to the laterally flared disc-shaped second metasomal segment, a feature unique among all known scorpions. The syntypes were all immatures, and not until 1960 did Vachon describe the morphology of an adult female collected by Wilfred Thesiger from Wadi Andhur in the Dhofar Province of Oman during one of his own camel treks across Arabia (Thesiger 1959). Additional records of the species have been published by Vachon (1979) and Hendrixson (2006) from Saudi Arabia, and Al Safadi (1992) from Yemen, all associated with sand systems in the central and southern regions of the Arabian Peninsula.

The genus *Apistobuthus* remained monotypic until Lourenço (1998) described a second species, *A. susanae*, from Ahvaz in the Khoozestan Province of Iran. The new species was distinguished from *A. pterygocercus* using four characters: trichobothrial pattern, dentition of the anal arc, pectinal tooth counts, and number of subrows of denticles on the pedipalp fingers. However, these characters are known to exhibit variation within scorpion populations, and since the species diagnosis was based on a single type specimen, the validity of this species needs to be confirmed. We recently collected a large series of *Apistobuthus* from several localities in Khoozestan Province (Navidpour et al. 2008) that bracket the type locality (Ahvaz) of *A. susanae*. Analysis of this material reveals that *A. susanae* is indeed distinct from *A. pterygocercus*, but new characters are required to differentiate the two species.

METHODS

Study specimens of *Apistobuthus susanae* and *A. pterygocercus* were collected in the field by means of ultraviolet light detection, or loaned by museums. Examination of cuticular morphology and photomacrography was facilitated by ultraviolet (UV) fluorescence imaging (Prendini 2003a, 2003b, 2004; Volschenk 2005) using an LED excitation source (Lowe et al. 2003). All anatomical photographs in the figures were taken with UV epifluorescence except for Fig. 17, which was taken with transmitted oblique illumination. Measurements were made with digital calipers or an eyepiece reticle, and generally followed the conventions of Lamoral (1979) and Sissom et al. (1990), with the following exceptions: carapace anterior width taken between most medial pair of lateral eyes; telson and vesicle lengths taken from anterior limit of vesicle, pedipalp chela length taken as chord length from external proximal end of manus to finger tips; pedipalp manus width and depth taken with articular condyles level; and metasoma III width excluding enlarged lateral spiniform granules. Carinal terminology follows Stahnke (1970), except that we follow the amendments to nomenclature of metasomal carinae introduced by Prendini (2001b, 2004). Trichobothrial terminology follows Vachon (1974, 1975), and hemispermatophore terminology follows Lamoral (1979). Statistics of samples are expressed as mean ± standard deviation (SD).

Abbreviations.—*Specimen depositories*: MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum, Basel, Switzerland; ONHM, Oman Natural History Museum, Muscat, Oman; RRLS, Razi Reference Laboratory of Scorpion Research, Ahvaz, Khoozestan, Iran; TERC, Terrestrial Environment Research Centre, Environment Agency, Abu Dhabi, United Arab Emirates; ZMUH, Zoologische Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany. *Private collections*: EV, Erich Volschenk, Western Australian Museum, Perth; FKCP, František Kovařík, Prague, Czech Republic; GL, Graeme Lowe, Philadelphia, Pennsylvania; MES, Michael E. Soleglad, Borrego Springs, California; VF, Victor Fet, Marshall University, West Virginia. *Biometrics*: L, length; W, width; D, depth.

Comparative material examined.—*Apistobuthus pterygocercus*: OMAN: 1 ♀, ca. 57 km S of Hafit, 23°29′N, 55°52′E, 200 m, 31 March 1994, M.D. Gallagher, B.J. Tigar MDG 8592 (NMB); 1 ♂, Ramlat Muqshin, 19°30.86′N, 54°36.71′E, 195 m, 6 October 1994, G. Lowe, M.D. Gallagher (ONHM); 1 ♂, 1 ♀, NW of Montesar, S of Wadi Muqshin, 19°29.17′N, 54°36.89′E, 200 m, 6 October 1994, G. Lowe, M.D. Gallagher (NMB); 2 ♀, Ramlat As Sahmah, 20°13.87′N, 55°54.75′E,

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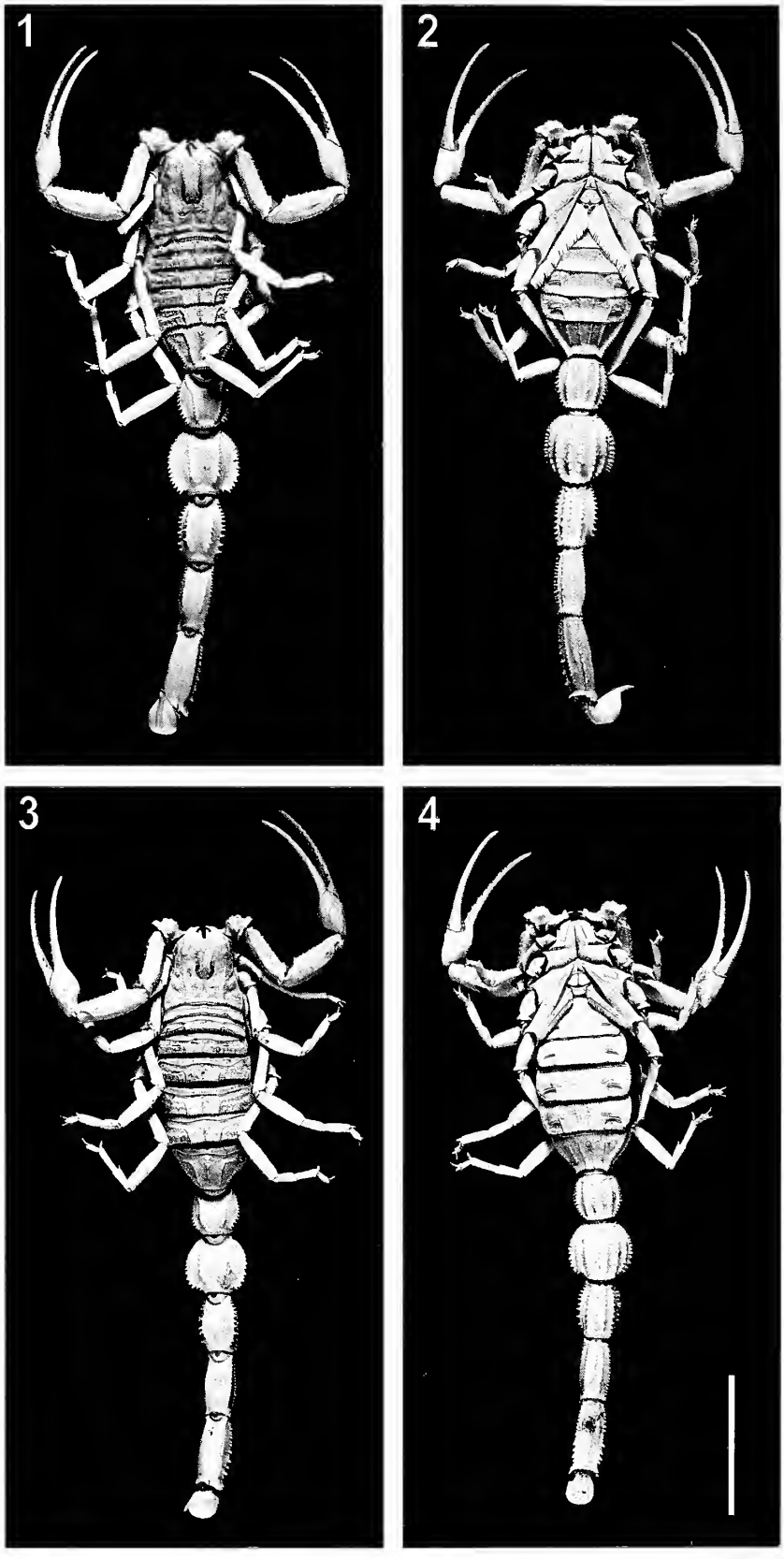
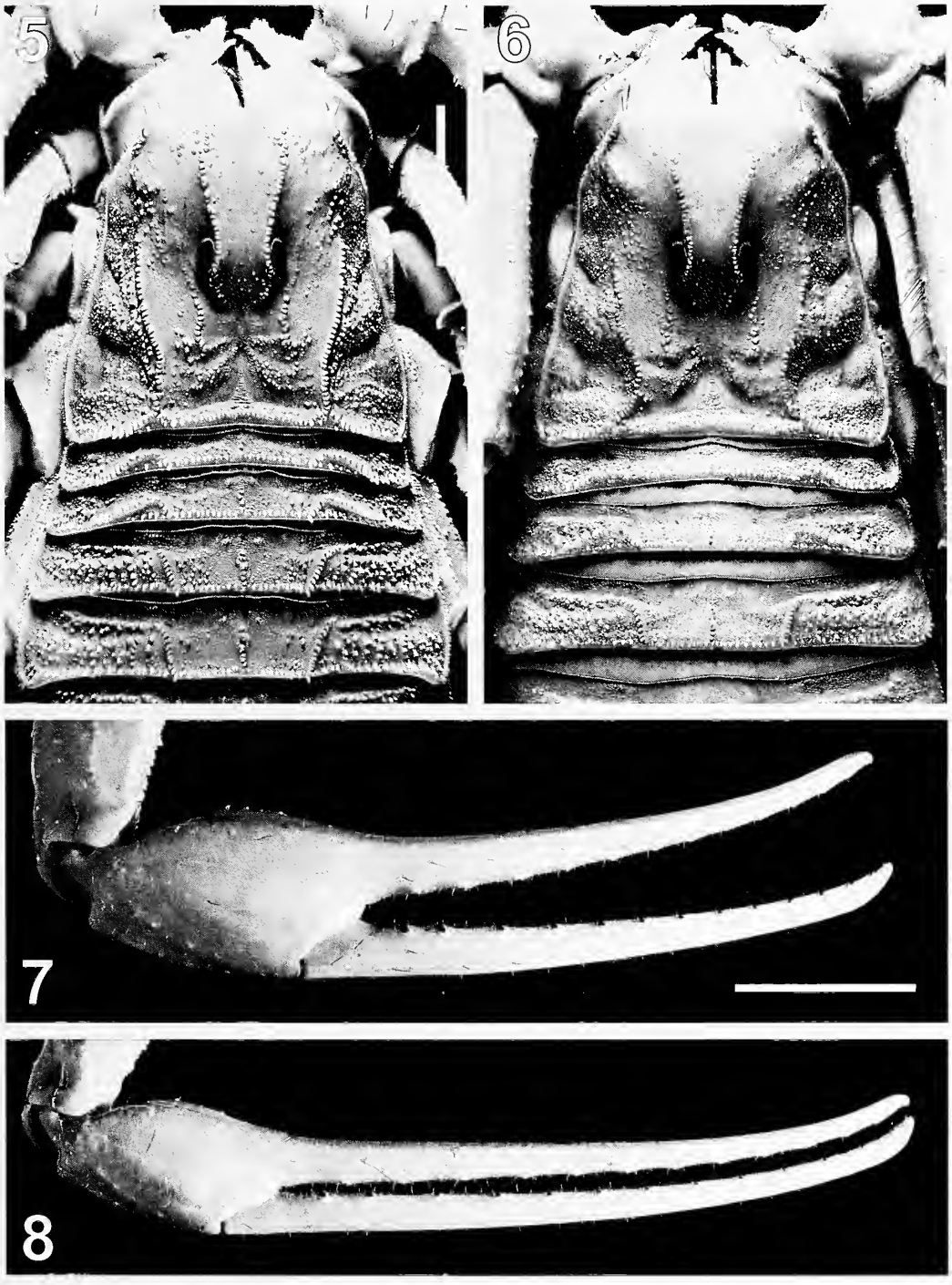
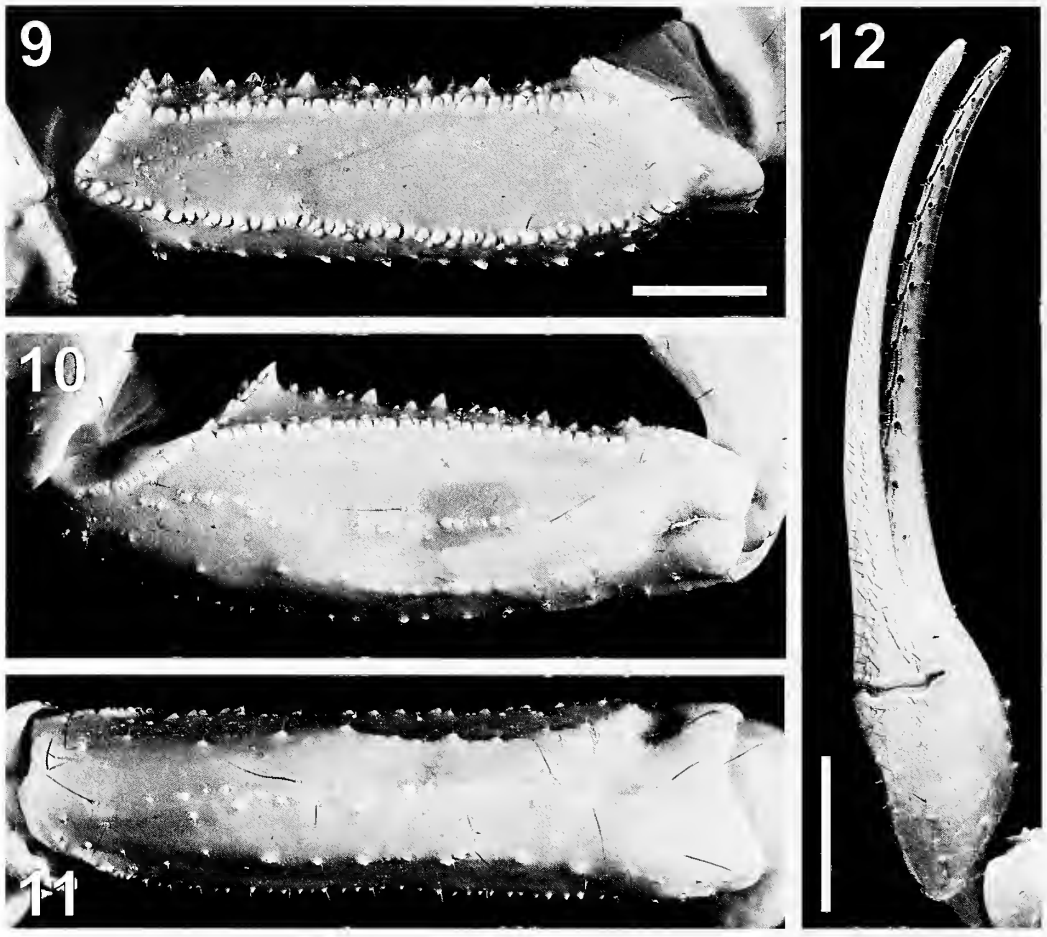


Figures 1–4.—*Apistobuthus susanae*, habitus. 1, 2 . Adult male from Bostan; 1. Dorsal aspect; 2. Ventral aspect; 3, 4. Adult female from Omidiyeh; 3. Dorsal aspect; 4. Ventral aspect. Scale bar = 20 mm.



Figures 5–8.—*Apistobuthus susanae*, adult male from Bostan, and *A. pterygocercus*, adult male from Uruq Al Hadd. 5, 6. Carapace and anterior tergites; 5. *A. susanae*, 6. *A. pterygocercus*, 7, 8. External aspect of pedipalp chela; 7. *A. susanae*; 8. *A. pterygocercus*. Vertical scale bar = 5 mm in 5, 4.87 mm in 6, horizontal scale bar = 5 mm in 7, 5.56 mm in 8.

165 m, 7 October 1994, G. Lowe, M.D. Gallagher (FKCP), 1 ♂, 1 ♀, Ramlat As Sahmah, 20°11.66′N, 55°57.41′E, 170 m, 7 October 1994, G. Lowe, M.D. Gallagher (NMB); 1 ♂, Ramlat Fasad, 18°32.44′N, 53°05.06′E, 240 m, May 1995, A. Dunsire (FKCP); 1 ♂, Wadi Atiyah, 18°17.09′N, 53°14.45′E, 260 m, 28 September 1995, G. Lowe, M.D. Gallagher, A. Dunsire (FKCP); 1 ♀, 55 km NW Ibri, 23°36.5′N, 56°05.33′E, 290 m, 22 November 1995, J. Dundon (GL); 1 ♀, Rub' al-Khali, Margandid, Montesar area, 19°36.85′N, 54°18.68′E, 1.XII.1995, J. Everett; 3 ♂, 1 ♀, Uruq al Hadd, Rub'Al Khali, 224 km WNW Thumrait, 18°53.6′N, 52°20.32′E, 11 January 1996, J.N. Barnes (EV, GL); 1 ♀, between Qarn Alan & Ghabah North, 21°22.03′N, 57°05.47′E, 150 m, 21 February 1996, M.D. Gallagher, MDG 8755 (NMB); 1 ♂, 1 ♀, 15 km NW of Shigag, 19°37.4′N, 54°04′E, 190 m, 30 November 1997, M.D. Gallagher & I.D. Harrison MDG 8909 (GL); 2 ♂, 15 km NNE. Fasad, 18°45.2′N, 53°08.9′E, 290 m, 29 January 1998, M.D. Gallagher, J.N. Barnes, MDG 8940 (ONHM). QATAR: 'Doha' (Ad Dawhah), 25°15″N, 51°34′E, 22 March 1963, A.J. Warr (MNHN RS4065). UNITED ARAB EMIRATES: 1 ♂, Zaid,



Figures 9–12.—*Apistobuthus susanae*, pedipalp, adult male from Bostan. 9. Pedipalp femur, dorsal aspect. 10. Pedipalp patella, dorsal aspect. 11. Pedipalp patella, external aspect. 12. Pedipalp chela, ventral aspect. Horizontal scale bar = 2 mm in 9, 2.15 mm in 10–11, vertical scale bar = 4 mm in 12.

dunes of Bada, Abu Dhabi, 9 July 1971, D.J.G. Williams (MNHN RS6509); 1 ♂, Bada Zaid, Abu Dhabi, dunes, March? 1972, D.J.G. Williams (MNHN RS6486); 1 ♀, Zaaba, camp area, dunes, 23°42.45′N, 55°29.33′E, June 1972, D.J.G. Williams (MNHN RS6940); 1 ♂, Zaaba, camp area, 23°42.45′N, 55°29.33′E, 12 July 1972?, D.J.G. Williams (MNHN RS6488); 2 ♀, Zaaba, camp area, 23°42.45′N, 55°29.33′E, 14 July 1972, D.J.G. Williams (MNHN RS6489, RS6942); 1 ♂, Khawr Fakhan, 25°20.47′N, 56°21.03′E, August 1972 (MNHN RS6490); 1 ♀, Dubai, 25°10.8′N, 55°15.6′E, September 1972, M.D. Gallagher, MDG 2185, (MNHN RS6485); 1 ♂, Juweiza, 25°20′N, 55°40′E, 8 March 1973, M.D. Gallagher MDG 2312 (MNHN RS6919); 1 ♂, Sweihan, 24°27.97′N, 55°19.88′E, 30 October 1993, (TERC).

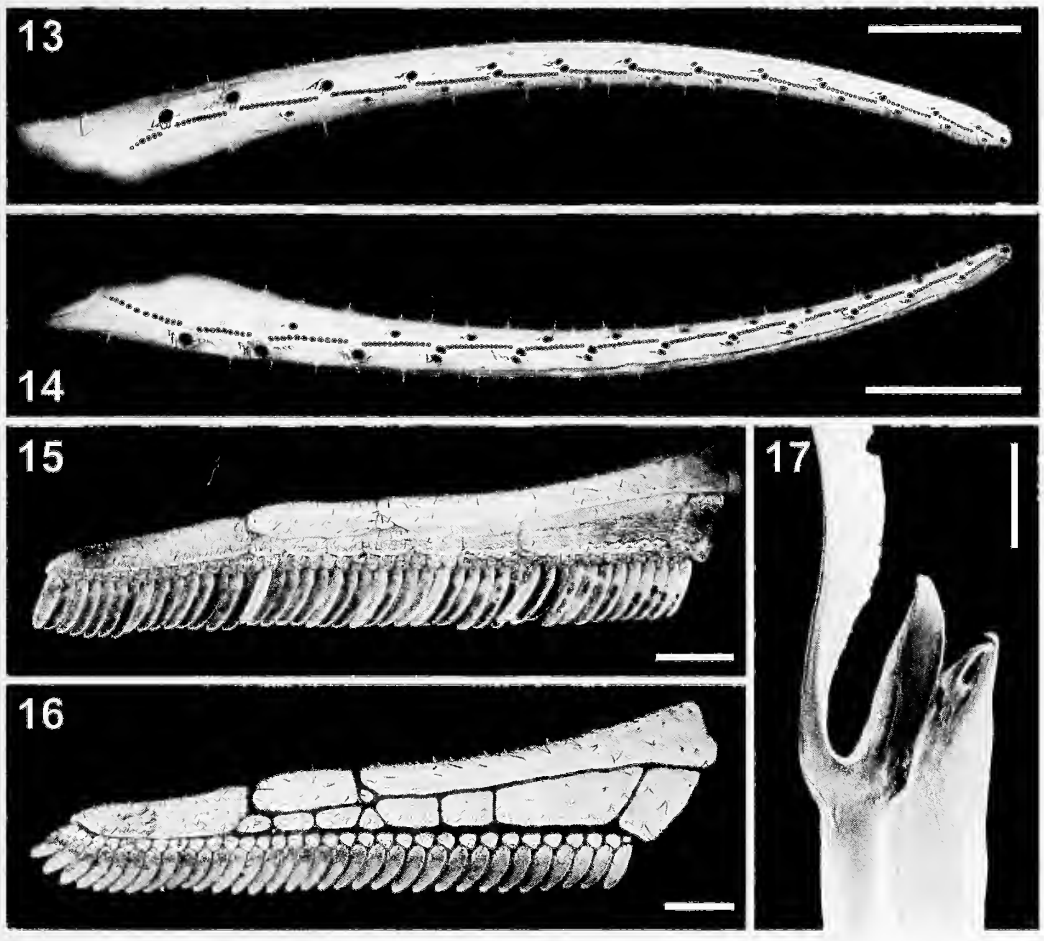
SYSTEMATICS

Family Buthidae C.L. Koch 1837
Apistobuthus Finnegan 1932

Apistobuthus Finnegan 1932:92.

Type species.—*Apistobuthus pterygocercus* Finnegan 1932

Diagnosis.—Medium to large buthids (Sissom 1990), adults 80–100 mm in length, carapace and tergites granulated; carapace with well developed anterior, superciliary, central median, central lateral, and posterior median carinae; posterior lateral carinae absent; anterior ocular region of carapace elevated relative to postocular region; tergites I–VI tricarinate, I–II with lateral carinae in a V-shaped configuration with two posteriorly directed arms; tergite VII with 5 carinae; metasoma elongate with segment II laterally dilated, disc-like; metasoma I with 10 denticulate carinae; metasoma II with 10 carinae, dorsosubmedian carinae denticulate, dorsolateral carinae strongly flared laterally, crenulate; median lateral, ventrolateral and ventromedian carinae smooth to vesiculate-granulate; metasoma III with 8 carinae bearing enlarged spiniform granules; metasoma IV with 8 moderately spinose carinae; metasoma V with 3 dentate carinae (ventromedian and paired ventrolateral); telson with bulbous vesicle lacking subaculear spine or tubercle, aculeus long, curved; pectines with fulcra; cheliceral fixed finger armed with two denticles on ventral surface; pedipalps orthobothriotaxic, type Aβ (Vachon 1974, 1975); chela smooth with carinae reduced or obsolete, fingers elongated, movable finger > 2.6 times chela manus ventral length; pedipalp fingers armed with linear subrows of primary denticles (normally 13 on fixed, 14 on movable), more distal subrows with proximal enlarged denticle; subrows flanked by internal and external accessory denticles; movable finger with two enlarged subdistal internal denticles; males without scalloping at base of pedipalp fingers; tibial spurs present or absent on legs III–IV; basitarsi I–III



Figures 13–17.—*Apistobuthus susanae*. 13, 14. Pedipalp chela dentition, adult male from Bostan; 13. Movable finger; 14. Fixed finger; 15. Right pectine, adult male from Albaji; 16. Right pectine, adult female from Omidiyeh; 17. Basal lobes of right hemispermatophore, dorsal aspect, compressed to separate lobes; adult male from Omidiyeh. Scale bars = 2.5 mm in 13–15, 1 mm in 16, 500 μm in 17.

with bristle-combs; telotarsi ventrally smooth, lacking mid-ventral spines or setae; all legs with prolateral and retrolateral pedal spurs.

Comparisons: The buthid genera *Buthus*, *Leiurus* and *Odontobuthus* share the following characters with *Apistobuthus*: ventrolateral carinae of metasoma V with enlarged dentition; telson bulbous without subaculear tubercle, tibial spurs developed on legs III–IV (variable in *A. pterygocercus*), chelicera with two denticles on ventral aspect of fixed finger, pedipalps orthobothriotaxic type Aβ, carapace with central lateral and posterior median carinae partially or completely fused in a lyre configuration. Additionally, both *Odontobuthus* and *Apistobuthus* have strongly modified ventromedian carinae on metasoma II–III, and *Odontobuthus*, *Leiurus* and *Apistobuthus* have lateral carinae on tergites I–II that are either V-shaped, or split into a pair of carinae (in the case of *Leiurus*). *Apistobuthus* differs from these genera in several presumably autapomorphic characters, including the modified form and carination of metasoma II–III, highly elongated pedipalps, higher range of pectinal tooth counts, and elevated anterior ocular region of the carapace.

Apistobuthus susanae Lourenço 1998
Figs. 1–4, 5, 7, 9–27, Tables 1–2

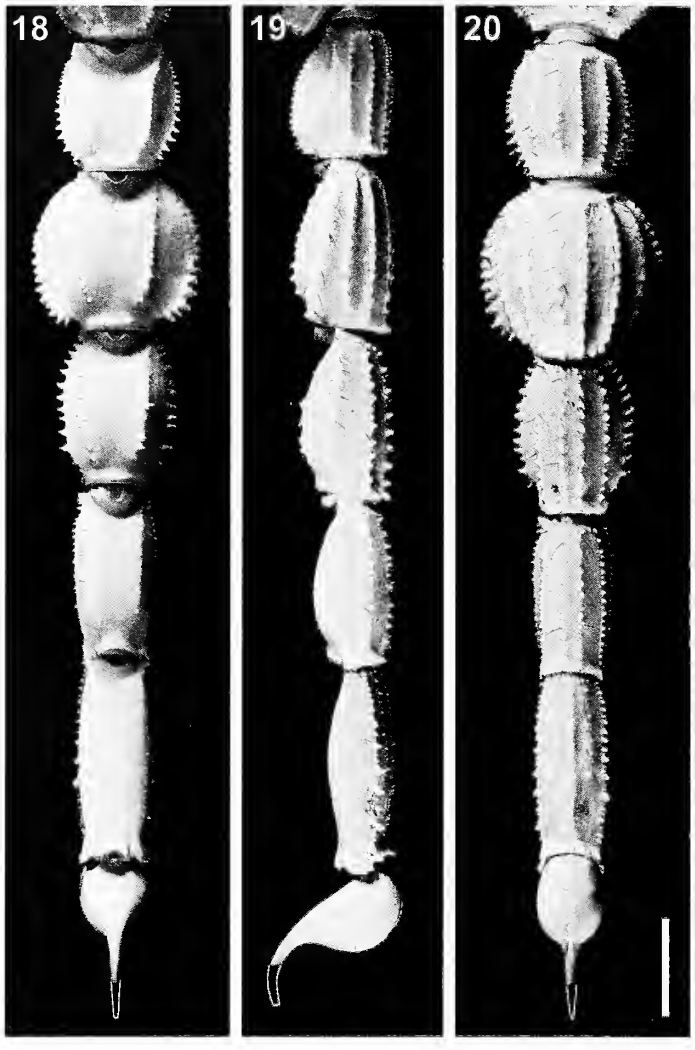
Apistobuthus sp.: Habibi 1971:45; Farzanpay 1988:36.

Apistobuthus susanae Lourenço 1998:238–244, figs. 8–14; Kovařík 1998:104; Fet & Lowe 2000:76; Navidpour et al. 2008:3–5, 7, 28, fig. 12.

Type specimen.—**Iran**: adult male, Ahvaz, summer 1961, T. Habibi (ZMUH A 27/98, not examined).

Material examined.—IRAN: *Khoozestan Province*: 2 ♂, 7 immature ♂, 3 immature ♀, Hamidiyeh, 31°27′57″N 48°29′18″E, 13 m, September 2007, Masihipour & Navidpour (NMB, RRLS, FKCP); 4 ♂, 3 immature ♂, 2 immature ♀, Bostan, 31°44′41″N 47°56′24″E, June 2007, Navidpour (NMB, VF, FKCP); 3 ♂, 3 ♀, 4 immature ♂, 4 immature ♀, Khoozestan Province, Omidiyeh, 30°57′49″N 49°31′47″E, Navidpour (NMB, RRLS, VF); 4 ♂, 4 ♀, Albaji, Ahvaz–Andimeshk road, 20 km to Ahvaz, 31°20′44″N 48°38′36″E, August 2005, Masihipour (NMB, GL, MES). KUWAIT: 1 ♀, "Koveit" (= Kuwait), D.A. Clayton (MNHN).

Diagnosis.—A species of *Apistobuthus* differentiated as follows: (1) pedipalp femur, patella and chela more robust than in *A. pterygocercus*, L/W ratios: femur 3.3–4.0 (n = 22), patella 2.5–3.3 (n = 22), chela 5.1–6.2 (n = 21) (Figs. 7, 9–12); pedipalp chela more inflated than in *A. pterygocercus*: manus W/carapace L 0.33–0.40 (n = 22); pedipalp fingers shorter: movable finger L/ carapace L 1.45–1.70 (n = 22), movable finger L/ chela manus ventral L 2.62–3.12 (n = 20); dentate margins of chela fingers usually bearing fewer primary



Figures 18–20.—*Apistobuthus susanae*, metasoma, adult male from Albaji. 18. Dorsal aspect; 19. Right lateral aspect; 20. Ventral aspect. Scale bar = 5 mm.

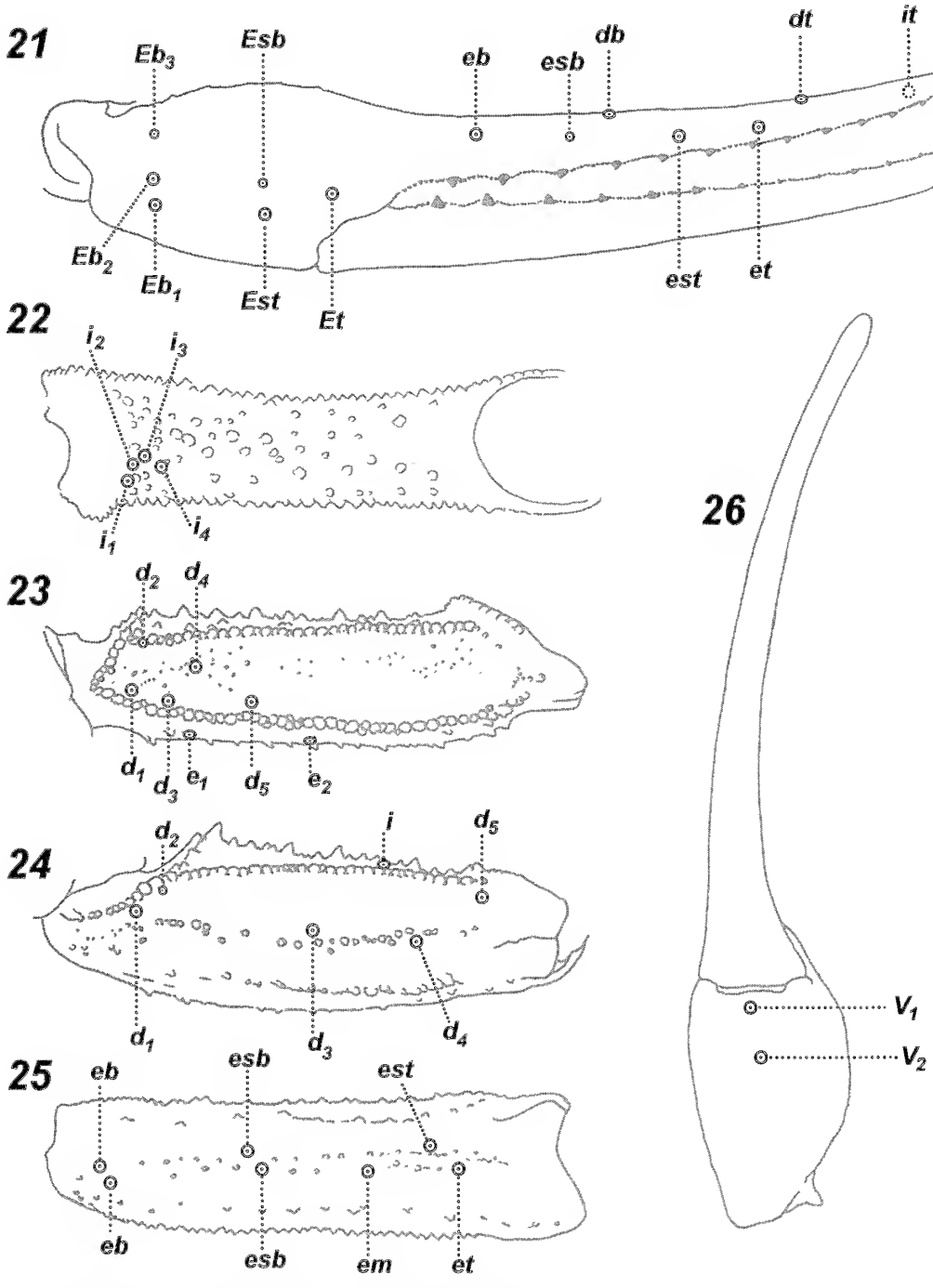
denticles than in *A. pterygocercus* (Figs. 13, 14); (2) pectines shorter than in *A. pterygocercus*, distal tips of pectines not extending past distal ends of coxa IV in females, and distal ends of trochanter IV in males; pectine teeth: males 42–48 (n = 41 combs), females 29–35 (n = 48 combs); (3) caparace and tergites with coarser granules and stronger carination than in *A. pterygocercus*; central lateral carinae of carapace strongly developed, fused with posterior median carinae to form a single continuous keel with gently curved lyre configuration (Fig. 5); (4) leg segments more robust than in *A. pterygocercus*: leg III patella L/D 3.1–3.8 (n = 21), ungues relatively short and stout; (5) metasoma II not as strongly flared as in *A. pterygocercus*: metasoma II W/ metasoma I W 1.35 ± 0.04, 1.29–1.41 (n = 21); with posterior enlargements of ventral carinae not overlapping metasoma III (Figs. 18–20).

In comparison, *A. pterygocercus* (Figs. 6, 8, 30–44, 46) differs as follows: (1) more slender pedipalps (Fig. 8): L/W ratios: femur 4.0–5.1, patella 3.4–4.5, chela 7.1–9.3 (n = 31) (Figs. 8, 34–36, 39); less inflated pedipalp chela: manus W/ carapace L 0.26–0.31 (n = 31); pedipalp fingers longer: movable finger L/ carapace L 1.69–2.08, movable finger L/ chela manus ventral L 3.64–4.63 (n = 31); fingers usually bearing higher numbers of primary denticles (Figs. 40, 41); (2) pectines extending up to or beyond distal ends of coxa IV (females) or trochanter IV (males); higher pectine tooth counts: males 49–59 (n = 34 combs), females 32–43 (n = 26 combs); (3) more moderately developed carination and finer granulation on the carapace and tergites; central lateral carinae of carapace weaker, may be partially broken, and often not fully fused and continuous with posterior median carinae; conjunction of central lateral and posterior median carinae forming a strongly curved lyre configuration (Fig. 6); (4) legs longer, more slender: leg III patella L/D 3.8.–4.4 (n = 13); tarsi with longer, more slender ungues (Fig. 46); (5) metasoma II with stronger lateral expansion: metasoma II W/ metasoma I W 1.47 ± 0.06, 1.36–1.61 (n = 31); ventral carinae of metasoma II more enlarged posteriorly, produced into angular protrusions overlapping anterior ventral margin of metasoma III (Figs. 42–44).

Morphometric differences between the two species for both sexes are summarized in Table 1. Comparative material representing *A. pterygocercus* that we analyzed was collected from a wide region spanning the southern margins of the Rub' al-Khali dunes, ranging from sites close to the two type localities along Thomas' route (Uruq adh Dhahiqah, Shena), across central Oman to Abu Dhabi in the United Arab Emirates (Fig. 27).

Etymology.—The species was named after Dr. Susan Finnegan who, as noted by Lourenço (1998), is the only female arachnologist to have described a new genus of scorpion. Dr. Finnegan also holds the distinction of being the first woman appointed to a post at the Natural History Museum in London. She succeeded Arthur Stanley Hirst in September 1927 as head of the Arachnida and Myriopoda Section, serving until her retirement in July 1936. Another scorpion, *Hottentotta finneganae* Kovařík 2007, was also named in her honor.

Redescription.—*Coloration*: entire body light yellow or light tan; carapace sometimes with variable dusky markings around median ocular tubercle, interocular triangle and carinae; ocular tubercle dark; telson aculeus and denticles of chelicerae and pedipalp fingers black. *Carapace* (Fig. 5): subrectangular, anterior W/posterior W 0.48–0.55 (n = 21); anterior half of carapace including median ocular tubercle elevated relative to posterior half; ocular tubercle broad, prominent, distance from anterior margin 0.43–0.48 times carapace length; anterior and superciliary carinae continuous, strong, granulose; anterior margin of carapace straight, rimmed with row of coarse granules, with < 10 macrosetae; linear array of 3–5 lateral eyes on each side, bordered with row of granules; central median carinae moderate, granulose; central lateral and posterior median carinae strong, granulose, fused into continuous keel; posterior margin of carapace rimmed with continuous row of granules, joined to posterior median carinae; lateral flanks of carapace steeply sloped; intercarinal areas studded with varying coarse to fine granulation. *Chelicera*: robust, manus with dorsal surface smooth proximally, with scattered granules distally, dorsointernal carina at base of fixed finger granular; ventral surface of manus smooth with sparse setation centrally, dense brush of setae on medial apical aspect and base of fixed finger; dentition following typical buthid pattern: fixed finger with large distal tine,



Figures 21–26.—*Apistobuthus susanae*, adult male from Bostan, map of trichobothrial pattern of right pedipalp. 21. Chela, external aspect; 22. Femur, internal aspect; 23. Femur, dorsal aspect; 24. Patella, dorsal aspect; 25. Patella, external aspect; 26. Chela, ventral aspect.

moderate subdistal denticle and large proximal bicusp on dentate margin, two prominent denticles on ventral aspect; movable finger with large dorsal distal tine, and shorter downward deflected ventral distal tine; dorsal margin of movable finger with two subdistal denticles and two small contiguous proximal denticles; ventral margin with two robust subdistal denticles. *Coxosternal area* (Figs. 2, 4): all coxae finely granular or shagreened; coxae II–III with granular anterior carinae; coxa IV with granular or crenulate anterior and posterior carinae; sternum triangular, coarsely granular, with deep median longitudinal sulcus; genital opercula granular on lateral surfaces, smooth medially. *Pectines* (Figs. 15, 16): basal piece with fine to coarse granulation medially, smooth laterally; distal tips of pectines not extending past distal ends of coxa IV in females, not past distal ends of trochanter IV in males; pectines with 3 marginal lamellae, 7–9 middle lamellae; pectine teeth of males 44–48 (n = 22 combs, mode = 46 with 8 combs), females 29–33 (*n* = 20 combs, mode = 32 with 8 combs). *Mesosoma* (Figs. 1–5): pretergites smooth; tergites I–VI tricarinate, median and lateral carinae strong, granular; posterior margins armed with row of granules; tergites I–II with lateral carinae in a V-shaped

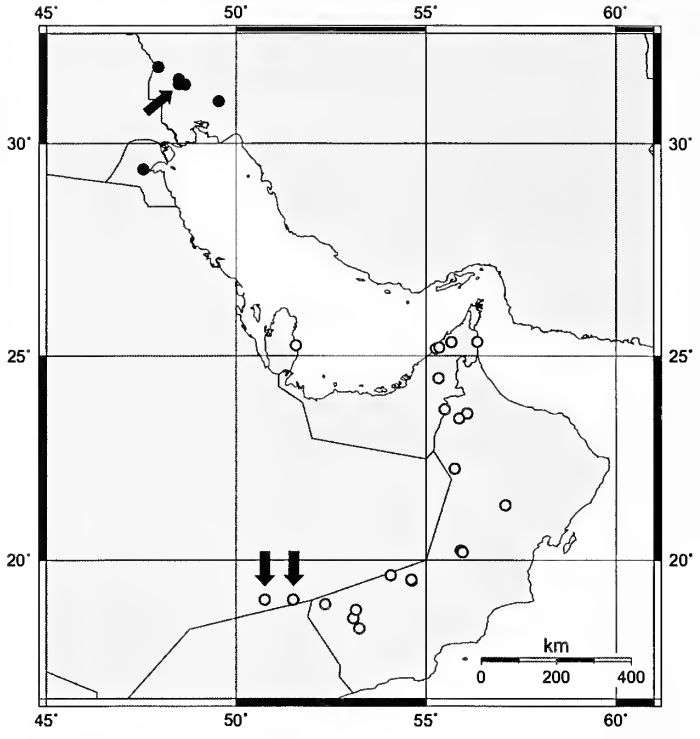


Figure 27.—Map of records for *Apistobuthus susanae* (closed circles) and *A. pterygocercus* (open circles). Coordinates of all material examined in this study are plotted, and also those for the holotype of *A. susanae* (diagonal arrow: Ahvaz, 31° 21.08′N, 48°38.3′E), and syntypes of *A. pterygocercus* (vertical arrows: Uruq adh Dhahiqah, Saudi Arabia, 19°00′N, 51°30′E; Shena, Saudi Arabia, 19°00′N, 50°45′E; coordinates from Thomas 1931). The record from Kuwait is plotted with approximate coordinates (29°24′N, 47°33′E).

configuration with two posteriorly directed arms; tergite VII with 5 carinae; medial intercarinal surfaces finely granular, lateral surfaces coarsely granular; tergite VII pentacarinate, all carinae strong, granular, medial intercarinal surfaces smooth, lateral surfaces sparsely granular; sternite III with 2 divergent carinae joined anteriorly; sternites IV–VII tetracarinate; all sternites shagreened or with dense, fine granulation; sternites IV–VI smooth behind spiracles; sternite VII smooth laterally; sternites III–VI with large slit-like spiracles; posterior and lateral margins of all sternites with row of fine granules or denticles. *Hemispermatophore* (Fig. 17): trunk long, slender; flagellum long, about equal in length to trunk when extended; inner lobe a broad blade, rounded apically; median lobe short, narrow; outer lobe short, tapered, apically flexed; basal lobe distinct, digitate; measurements (male from Omidiyeh): trunk L (to base of flagellum) 11.4 mm, pars recta 4.4 mm, inner lobe (from base of flagellum) 960 μm, median lobe 415 μm, outer lobe 360 μm, basal lobe 100 μm. *Metasoma* (Figs. 18–20): metasoma I with 10 denticulate carinae; metasoma II with 10 carinae, dorsosubmedian carinae denticulate, dorsolateral carinae strongly flared, crenulate to denticulate with enlarged serrate armature posteriorly; median lateral, ventrolateral and ventromedian carinae robust, thickly sclerotized, smooth to vesiculate-granulate; ventromedian carinae with posterior granules enlarged, tuberculiform, not projecting over metasoma III; metasoma III with 8 carinae, armed with enlarged, sharp conical denticles or spiniform granules; metasoma IV with 8 carinae; dorsosubmedian and dorsolateral carinae weak, with small dentate granules; ventrolateral and ventromedian carinae strong, denticulate; metasoma V with dorsolateral carinae smooth or obsolete, ventrolateral and unpaired ventromedian carinae strong, denticulate; ventrolateral carinae with larger posterior denticulations separated by finer denticulations; ventrosubmedian carinae weak, confined to anterior 2/3 of metasoma V, marked by broad strip of fine and coarse granules; metasoma I–III with all intercarinal surfaces smooth; metasoma IV–V with dorsal and lateral surfaces smooth, ventral surfaces finely shagreened. *Telson* (Figs. 18–20): vesicle bulbous, smooth, lacking subaculear spine or tubercle; aculeus long, curved. *Pedipalp femur* (Fig. 9): dorsoexternal, dorsointernal, and ventrointernal carinae strong with dentate granules; exterior median carinae weak to obsolete, marked by dispersed row of granules and scattered long macrosetae; ventroexternal carina obsolete,

Table 1.—Morphometric differences between *Apistobuthus susanae* and *A. pterygocercus*. Sample size for each range of values is given in brackets as number of individuals for morphometric ratios, and number of combs or fingers for pectine teeth and denticle counts, respectively. Sample sizes marked with an asterisk (*) indicate that published data for the holotype female of *A. susanae* was included in the parameter ranges. Denticle counts enumerate the non-enlarged primary denticles, and exclude cases of teratology, abnormal development, fusion or splitting of subrows that result in more or less than 13 subrows (fixed finger) or 14 subrows (movable finger). Data are from adults except for number of pectine teeth, which is independent of age.

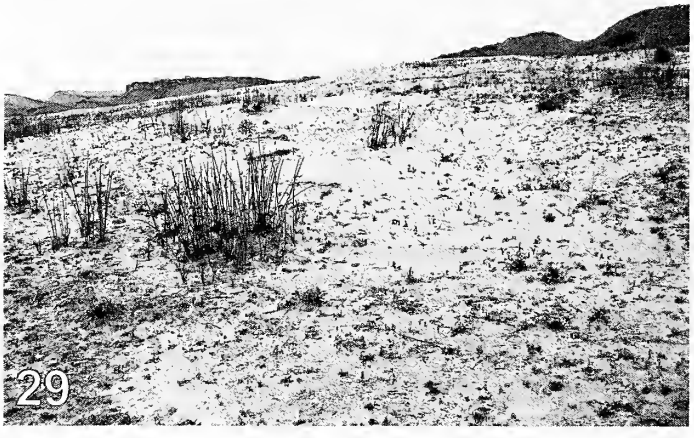
	Males		Females	
	A. susanae	*A. pterygocercus*	*A. susanae*	*A. pterygocercus*
Pedipalp femur L/W	3.52–4.02 (11)	4.13–5.10 (18)	3.29–4.02 (11*)	4.01–4.83 (13)
Pedipalp patella L/W	2.92–3.27 (11)	3.61–4.49 (18)	2.58–3.23 (11*)	3.40–4.00 (13)
Pedipalp chela L/manus W	5.54–6.19 (11)	7.61–9.25 (18)	5.06–6.00 (10*)	7.17–8.09 (13)
Pedipalp movable finger L/chela manus ventral L	2.62–3.01 (11)	3.64–4.33 (18)	2.76–3.12 (9)	3.78–4.63 (13)
Pedipalp movable finger L/manus W	4.28–4.86 (11)	6.10–7.75 (18)	3.89–4.67 (11*)	5.77–6.73 (13)
Pedipalp chela manus ventral L/manus W	1.48–1.70 (11)	1.56–1.80 (18)	1.39–1.60 (9)	1.25–1.65 (13)
Pedipalp movable finger L/carapace L	1.55–1.62 (11)	1.69–2.08 (18)	1.45–1.70 (11*)	1.75–2.02 (13)
Pedipalp manus W/carapace L	0.33–0.38 (11)	0.26–0.31 (18)	0.35–0.40 (11*)	0.29–0.31 (13)
Leg III patella L/W	3.44–3.80 (11)	4.03–4.37 (6)	3.16–3.73 (9)	3.82–4.17 (7)
Pectine teeth	42–48 (41)	49–59 (34)	29–35 (48*)	32–43 (26)
Fixed finger primary denticles	143–166 (16)	156–198 (29)	142–163 (17)	164–202 (23)
Movable finger primary denticles	155–172 (18)	164–203 (31)	146–166 (16)	166–207 (22)

Table 2.—*Apistobuthus susanae*, measurements of representative adult male and female (lengths in mm).

	Male, Bostan	Female, Omidiyeh
Total L	88.00	91.00
Metasoma + Telson L	58.30	56.00
Carapace L/ anterior W/ posterior W	10.43/ 5.83 /10.82	10.70/ 6.29/ 12.73
Median ocular tubercle to anterior margin	4.73	4.72
Metasoma I L/ W/ D	7.37/ 7.67/ 5.66	7.31/ 7.61/ 5.63
Metasoma II L/ W/ D	9.07/ 10.36/ 5.77	9.50/ 9.83/ 5.57
Metasoma III L/ W/ D	9.20/ 5.81/ 5.08	9.69/ 6.40/ 5.30
Metasoma IV L/ W/ D	9.81/ 4.57/ 4.25	9.18/ 5.17/ 4.88
Metasoma V L/ W/ D	12.00/ 4.70/ 3.67	11.60/ 5.04/ 4.08
Telson L	10.30	10.32
Vesicle L/ W/ D	5.71/ 4.36/ 3.75	5.91/ 4.44/ 4.27
Pedipalp chela L	21.66	21.61
Pedipalp chela chela manus ventral L	5.72	6.03
Pedipalp chela manus W/ D	3.52/ 4.23	4.02/ 4.59
Pedipalp chela fixed finger L/ movable finger L	14.63/ 16.92	14.38/ 16.67
Pedipalp femur L/ W	10.45/ 2.77	10.14/ 2.70
Pedipalp patella L/ W	11.66/ 3.68	11.62/ 3.68
Pectine L	13.32	9.01
Pectine teeth Left/Right	46/ 47	32/ 33
Ventral anal arc, denticles	8	8
Movable finger primary denticles, Left/ Right	160/ 163	160/ 161
Fixed finger primary denticles, Left/ Right	154/ 153	154/ 148
Leg III patella, L/ D	9.80/ 2.58	9.63/ 2.75

marked on distal half by row of short macrosetae; dorsal surface of femur smooth except for scattered small granules on proximal area, ventral surface smooth except for proximal cluster of granules, internal surface studded with large conical granules interspersed with small granules. *Pedipalp patella* (Figs. 10, 11): dorsointernal, ventrointernal, and ventromedian carinae strong, with dentate granules; internal surface with dorsal patellar spur carinae bearing enlarged dentate granules interspersed with smaller dentate granules, and several long macrosetae; ventroexternal carina weak with sparse low granules; exterior median carina moderate with irregular granules; dorsomedian and dorsoexternal carinae weak to moderate with irregular small to large granules; intercarinal surfaces of patella mostly smooth, only lightly shagreened in small areas. *Pedipalp chela* (Figs. 7, 12): smooth; dorsomarginal, digital, and external secondary carinae weak, smooth; ventroexternal carinae weak to moderate, smooth; manus slightly inflated, fingers long and tenuous; fixed finger normally with 13 subrows of primary denticles, movable finger normally with 14 subrows; proximal enlarged primary denticle normally absent on proximal 4 subrows of fixed finger, proximal 5 subrows of movable finger; denticle subrows on fingers flanked by enlarged external accessory denticle, sometimes reduced or absent on distal 1–2 subrows; all denticle subrows flanked by internal accessory denticle, ventral surface of manus with up to a dozen moderate length macrosetae; ventral surface of movable finger with abundant short, fine macrosetae. *Trichobothrial pattern*: orthobothriotaxic type Aβ, with full complement of normal and petite trichobothria (Figs. 21–26); femur with d_2 on dorsal surface, patella with d_3 internal to dorsomedian carina, chela fixed finger with *esb* and *eb* situated between *db* and *dt*. *Legs*: moderately slender, segments with granular carinae; femur I–III, patella I–III and femur IV with strongly denticulate ventral carinae; tibia I —III and basitarsi I —III with prominent bristle-combs on retrolateral margins, and many long macrosetae on prolateral margins; prolateral and retrolateral pedal spurs setose, not bifurcated (Fig. 45). *Measurements*: data from representative male and female specimens are cited in Table 2.

Variation.—*Adults*: sexual dimorphism: males differ from females in having longer, pectines (pectine L/ carapace L, males 1.28–1.45, females 0.82–0.90), and longer pectine teeth that overlap basally; more robust carination and coarser granulation on carapace, tergites, and sternites; median carinae on sternites IV–V moderate, granular in males, weak to obsolete, smooth in females; in morphometrics, males as a group have slightly more slender pedipalps and legs, and a more elongated carapace (cited are means ± SD, n = sample size, U and $P < 0.05$ values from Mann–Whitney test): pedipalp femur L/W, male 3.80 ± 0.16 (11), female 3.65 ± 0.16 (10), $U = 24$, $P = 0.03$; chela L/W, male 5.91 ± 0.24 (11), female 5.52 ± 0.32 (9), $U = 16$, $P = 0.01$; pedipalp chela manus ventral L/manus W, male 1.62 ± 0.07 (11), female 1.48 ± 0.06 (9), $U = 9$, $P = 0.002$; chela manus W/D, male 0.84 ± 0.03 (11), female 0.87 ± 0.02 (10), $U = 20$, $P = 0.014$; chela movable finger L/manus W, male 4.60 ± 0.20 (11), female 4.33 ± 0.27 (10), $U = 25$, $P = 0.035$; leg III patella L/W, male 3.61 ± 0.10 (11), female 3.43 ± 0.16 (9), $U = 15$, $P = 0.009$; carapace L/W, male 0.92 ± 0.03 (11), female 0.89 ± 0.03 (10), $U = 24$, $P = 0.03$. *Morphometric ratios*: both sexes pooled (n = sample size): carapace L/W 0.84–0.96 (21), median ocular tubercle to anterior margin/ carapace length 0.43–0.48 (21), metasoma I L/W 0.91–1.05 (21), metasoma II L/W 0.82–0.97 (21), metasoma III L/W 1.23–1.66 (21), metasoma IV L/W 1.78–2.15 (21), metasoma V L/W 2.30–2.78 (21), pedipalp femur L/W 3.49–4.02 (21), pedipalp patella L/W 2.58–3.27 (21), pedipalp chela L/W 5.06–6.19 (20), pedipalp chela manus W/D 0.78–0.91 (21), pedipalp chela manus ventral L/chela W 1.39–1.70 (20), pedipalp movable finger L/chela manus ventral



Figures 28, 29.—Habitat of *Apistobuthus susanae*. 28. Site at Omidiyeh; 29. Site at Bostan.

L 2.62–3.12 (20), pedipalp fixed finger L/chela manus ventral L 2.22–2.70 (20), pedipalp chela manus W/carapace length 0.33–0.40 (21), pectine L/carapace L 0.82–1.45 (21), leg III patella L/W 3.16–3.80 (20), pedipalp movable finger L/carapace L 1.45–1.69 (21), pedipalp femur L/carapace L 0.90–1.06 (21), pedipalp patella L/carapace L 1.02–1.18 (21). *Juveniles*: similar to adults, but with less pronounced lateral expansion of metasoma II.

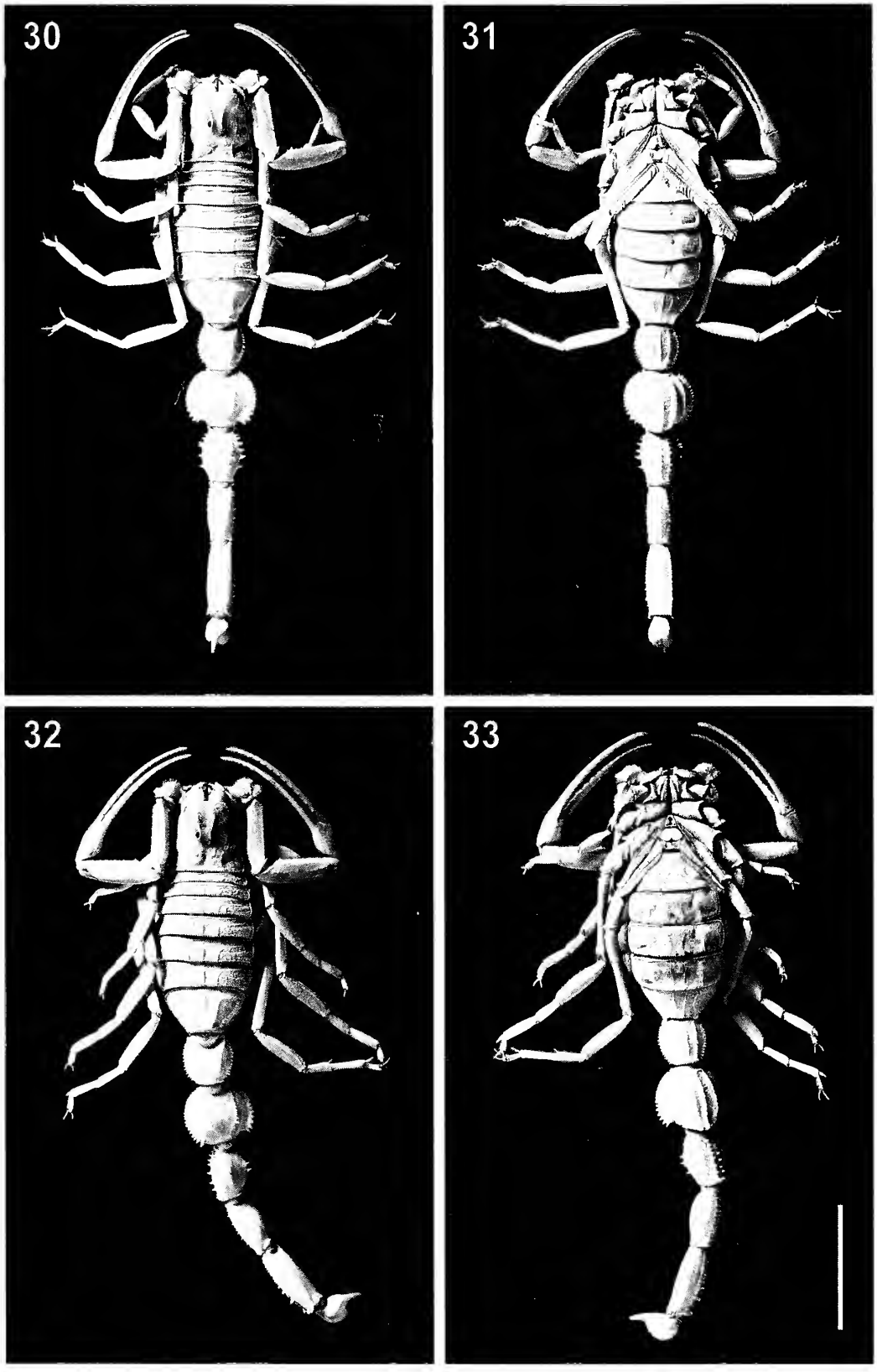
Although we have not examined the holotype female from Ahvaz, it is an adult (carapace L = 10.2 mm) and, based on the morphometric data provided by Lourenço (1998), it is clearly grouped with our sample from the region of Khoozestan Province surrounding Ahvaz, and is distinguishable from *A. pterygocercus*: pedipalp movable finger L/manus W 4.33, pedipalp femur L/W 3.29, pedipalp patella L/W 3.03, pedipalp chela L/W 5.85, pedipalp manus W/carapace L 0.39, pedipalp movable finger L/carapace L 1.70. In addition to the Khoozestan material, an adult female from Kuwait, previously loaned from MNHN and examined, is also assigned here to *A. susanae* on the basis of morphometric diagnostic characters: pectine teeth 33/32, pedipalp femur L/W 3.61, pedipalp patella L/W 2.73, pedipalp movable finger L/chela W 4.67, pedipalp chela W/carapace L 0.36, pedipalp movable finger L/carapace L 1.69.

The majority of our *Apistobuthus* material originates from sample sites that are widely separated geographically. However, one adult male that we analyzed was labeled "Doha, Qatar," which is situated roughly midway between Ahvaz and Uruq adh Dhahiqah, the type localities for the two species (Fig. 27, open circle). Morphometric data for this specimen is consistent with our series of *A. pterygocercus* from southern Rub' al Khali: pedipalp movable finger L/manus W 6.54, pedipalp femur L/W 4.32, pedipalp patella L/W 3.61, pedipalp chela L/W 8.22, pedipalp manus W/carapace L 0.26, movable finger L/ chela manus ventral L 3.64, pectine teeth 51/49, fixed finger primary denticles 170/171, and movable finger primary denticles 186/180. Vachon (1979) illustrated a specimen from Al Khardj, southeast of Riyadh, another intermediate locality. In Vachon's fig. 5, the pedipalps appear very slender and fall well within our observed range of variation of *A. pterygocercus*. Thus there is no evidence for clinal variation that might bridge morphometric differences between the two species and lead us to synonymize them.

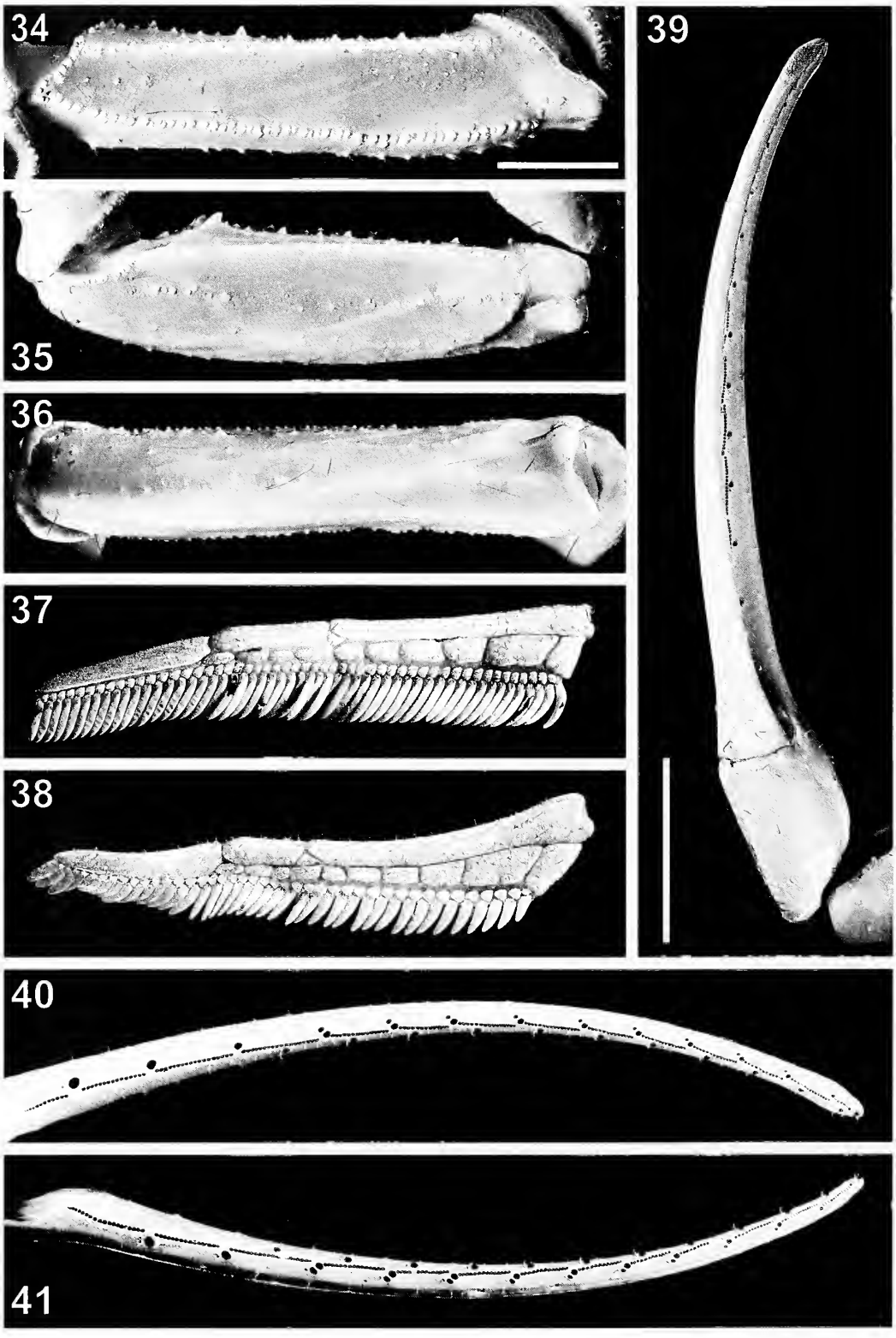
Habitat.—As reported by Navidpour et al. (2008), *A. susanae* collection sites in Khoozestan were restricted to hot, sandy desert at elevations < 35 m (Figs. 28, 29). These sites, along with the record from Kuwait, are situated on a broad alluvial fan around the Tigris-Euphrates River delta (Fig. 27). The substrate consists of sandy soils stabilized by vegetation with low sand hills and nabkha dunes suitable for arenicolous fauna. The habitat of *A. susanae* contrasts with the tall aeolian dunes of Rub' al-Khali, the domain of *A. pterygocercus*. Thomas (1931) vividly portrayed the terrain he encountered at the type locality of *A. pterygocercus*:

> "Uruq Dhahiya, a great immensity of dune country. Vast ridges rise to towering heights; about them are precipitous gorges. It is almost impassable. Again and again we were driven to dismount and to scoop footholds with our hands in the soft yielding slope, so that our camels could climb."

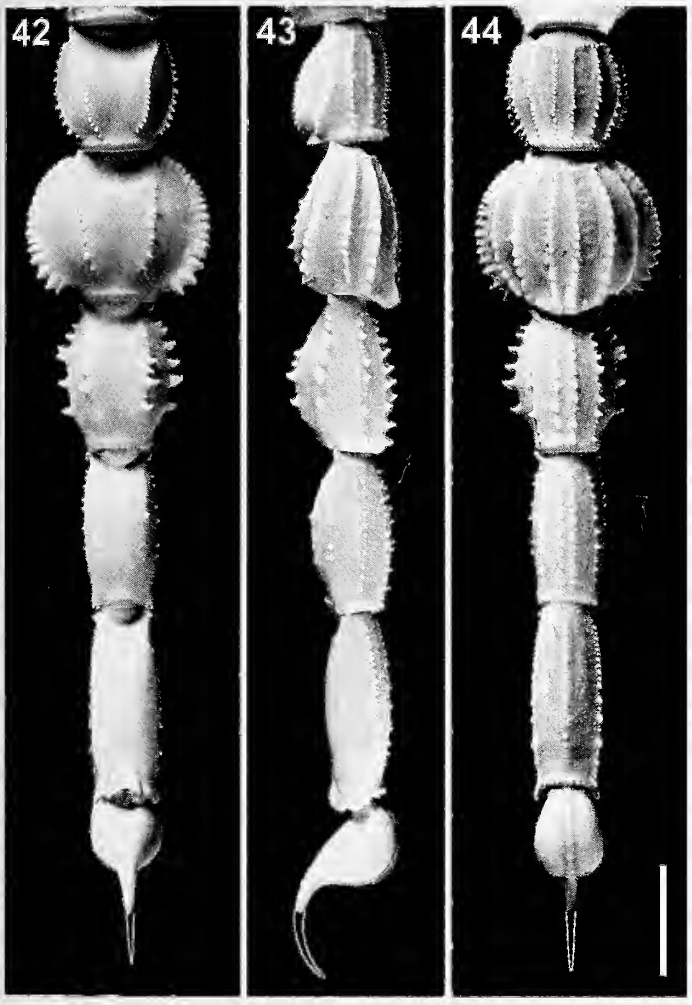
Both species of *Apistobuthus* fit the psammophilous ecomorphotype (Polis 1990; Fet et al. 1998; Prendini 2001a), with long legs and compressed tarsi bearing bristle-combs. Some of the distinguishing features of *A. pterygocercus* may be ultrapsammophilous specializations that evolved to cope with life in less compact wind-blown sands. The longer legs and ungues would enhance traction on soft sand, and also increase the baseline for Rayleigh wave triangulation of prey (Brownell 1977). The latter effect, together with the longer pedipalp fingers, is likely to increase the chances of capturing more sparsely distributed prey in austere dune environments. The adaptive significance of other traits, such as longer pectines, reduced carination, more enlarged metasoma II, and degenerated tibial spurs is unclear. It was speculated that the flared metasoma II with heavily sclerotized lateral and ventral carinae, and the array of sharp spiniform granules on metasoma III, could shield *Apistobuthus* from rear attack by predators while inside a burrow (Lowe 1993). The use of part of the body as a protective barrier inside a burrow is termed "phragmosis," a well known example of which is the function of the disc-shaped abdomen in the trapdoor spider genus *Cyclocosmia* Ausserer 1871 (Gertsch & Wallace 1936; Gertsch & Platnick 1975; Hunt 1976).



Figures 30–33.—*Apistobuthus pterygocercus*, habitus. 30, 31. Adult male from Uruq al Hadd; 30. Dorsal aspect; 31. Ventral aspect; 32, 33. Adult female from 55 km NW Ibri; 32. Dorsal aspect; 33. Ventral aspect. Scale bar = 20 mm.



Figures 34–41.—*Apistobuthus pterygocercus*. 34. Pedipalp femur, dorsal aspect; 35. Pedipalp patella, dorsal aspect; 36. Pedipalp patella, external aspect; 37. Right pectine, adult male; 38. Right pectine, adult female; 39. Pedipalp chela, ventral aspect; 40, 41. Pedipalp chela dentition; 40. Movable finger; 41. Fixed finger. Figs. 34–37, 39: adult male from Uruq al Hadd; Figs. 40, 41: adult male from Wadi Atiyah; Fig. 38: adult female from Margandid. Horizontal scale bar = 2.5 mm in 34, 2.9 mm in 35 & 36, 3.8 mm in 37, 2.4 mm in 38. Vertical scale bar = 5.5 mm in 39, 3.7 mm in 40, 4 mm in 41.

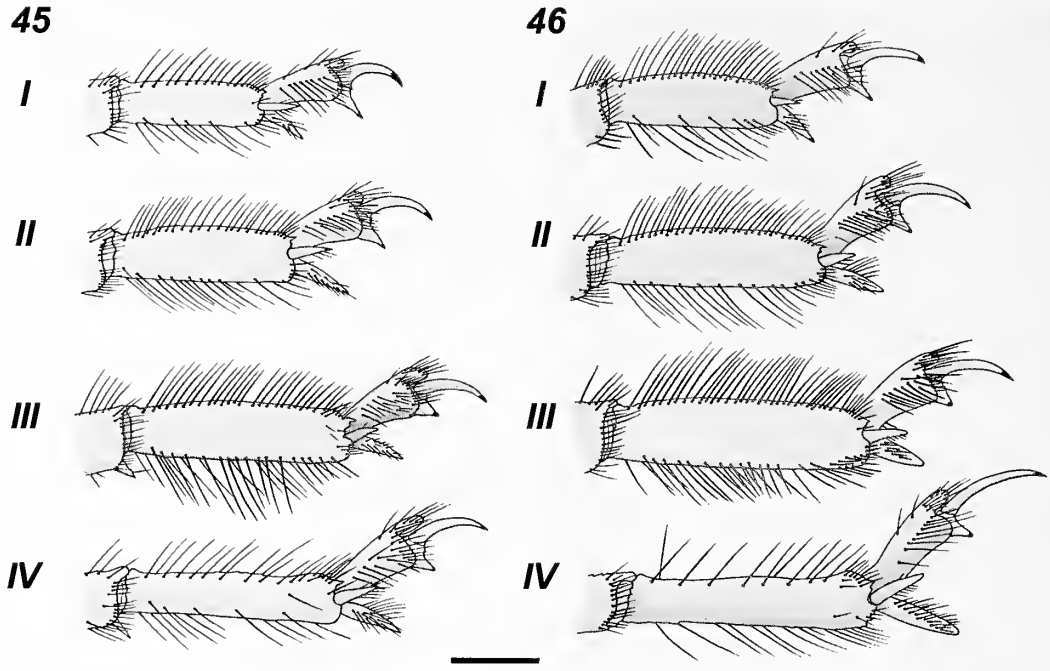


Figures 42–44.—*Apistobuthus pterygocercus*, metasoma, adult male from Uruq al Hadd. 42. Dorsal aspect; 43. Right lateral aspect; 44. Ventral aspect. Scale bar = 7 mm.

Distribution.—The species is known only from Khoozestan Province in South-western Iran, and Kuwait.

Remarks.—Lourenço (1998) correctly recognized the single type specimen from Ahvaz as belonging to a new species of *Apistobuthus*, and he cited four characters that he believed could differentiate it from *A. pterygocercus*. We have analyzed each of these based on larger sample sizes, and we conclude that they cannot serve as reliable diagnostic characters. (1) *Trichobothrial pattern*: the holotype of *A. susanae* was cited as being neobothriotaxic, with trichobothria d_2 and *est* absent on the pedipalp patella. We found that d_2 was small but certainly present on 40/40 pedipalp patellae (n = 20 adults) of *A. susanae* (and present on 62/62 patella from n = 31 adult *A. pterygocercus*). The areolar socket and seta of d_2 were clearly visible under ultraviolet fluorescence microscopy, but were more difficult to resolve under reflected light microscopy and this may have led to erroneous reports of the loss of this petite trichobothrium. In *A. susanae*, 38/40 pedipalp patellae (n = 20 adults) were orthobothriotaxic, bearing all 7 external trichobothria. There were 2/40 cases of trichobothrial loss (n = 2 adults): one patella with *est* lost (unilaterally, right patella), and one patella with esb_1 and esb_2 lost (also right patella). Thus, neobothriotaxy in *A. susanae* is a teratological condition, not representative of the population. We note that *A. pterygocercus* patellae are also normally orthobothriotaxic (59/62 patellae with 7 external trichobothria). (2) *Anal arc dentition*: the holotype of *A. susanae* has 10 teeth on the ventral anal arc, and *A. pterygocercus* was cited as having only 4 teeth. We analyzed the number of major teeth on the ventral anal arc, not including the lateral anal lobe and excluding small denticles that sometimes occurred between the larger major denticles. The number of teeth for *A. susanae* was: 8.20 ± 1.36, range 6–12 (n = 20); for *A. pterygocercus* it was: 8.16 ± 1.44, range 5–11 (n = 31). There was no significant difference in number of anal arc teeth between the two species (U = 293.5, P = 0.75, Mann-Whitney test). (3) *Pectinal tooth count*: the holotype female of *A. susanae* has 29 and 30 pectine teeth, lower than the range of 36–38 cited by Lourenço for females of *A. pterygocercus*. Analysis of our samples shows that *A. pterygocercus* does indeed exhibit higher average numbers of pectine teeth in both sexes (Table 1). However, in our samples the ranges of pectinal tooth counts of females of the two species overlap: 35 is the upper count for *A. susanae*, 32 the lower count for *A. pterygocercus*. Hence, this character is insufficient to diagnose and differentiate the species. (4) *Primary denticle subrows*: the number of subrows on the pedipalp chela fingers was cited as 12 for *A. susanae* versus 14 for *A. pterygocercus*. This characterization does not take into account the fact that in *Apistobuthus* there is a significant difference in the number of subrows for fixed and movable fingers. In a sample of n = 20 adults of *A. susanae*: 37 intact fixed fingers included 32/37 with 13, 2/37 with 12, 2/37 with 11, and 1/37 with 9 subrows; 37 intact movable fingers included 33/37 with 14, 3/37 with 13, and 1/37 with 8 subrows. In a sample of n = 31 adults of *A. pterygocercus*: 60 intact fixed fingers included 3/60 with 14, 53/60 with 13, 2/60 with 12, 1/60 with 11 and 1/60 with 9 subrows; 61 intact movable fingers included 1/61 with 15, 52/61 with 14, 3/61 with 13, 1/61 with 12, 2/61 with 10, 1/61 with 8 and 1/61 with 7 subrows. Thus, excluding a minority of cases involving subrow fusions associated with teratology or finger regeneration after injury, the normal subrow counts are 13 fixed and 14 movable for both species. There was no statistical difference between subrow counts in samples taken from the two species, either for fixed (U = 985.5, P = 0.36) or movable fingers (U = 1114, P = 0.92) (Mann-Whitney test).

On the type specimen of *A. susanae*, Lourenço (1998) noted that petite trichobothrium d_2 on the femur was "very small and placed almost on the internal surface," and actually depicts d_2 on the internal side of the dorsointernal carina (in his fig. 12). We invariably observed a very small seta at the expected location of d_2, and it could be identified as a petite trichobothrium only by having a slightly larger areola compared to the series of presumably chemotactic microsetae deployed along the dorsointernal carina. This presumed d_2 was always clearly positioned on the dorsal surface of the femur, adjacent to granules of the dorsointernal carina, and never on the internal surface. Lourenço (1998) also stated that the β-configuration (Vachon 1975) of femoral trichobothria in the *A. susanae* type specimen was "somewhat atypical" in the genus *Apistobuthus*. We found a β-configuration in all specimens examined of both *A. susanae* and *A. pterygocercus*. Together with the position of patellar d_3, this confirms



Figures 45, 46.—Legs I–IV basitarsus and telotarsus, retrolateral aspect. 45. *Apistobuthus susanae*, adult male from Albaji; 46. *Apistobuthus pterygocercus*, adult male from Wadi Atiyah. Scale bar = 2 mm.

placement of *Apistobuthus* in the "Buthus" group of Fet et al. 2005.

The presence or absence of tibial spurs on legs III–IV is a character with taxonomic value at the genus level (Sissom 1990), and the secondary reduction or loss of tibial spurs occurs in a number of psammophilous scorpions (Fet et al. 2001). We analyzed this character in *Apistobuthus*, scoring a "loss" if the tibial spur was either absent or degenerated to a very small vestigial spur (< 20% the length of a fully developed spur). We found that tibial spur degeneration or loss was infrequent in *A. susanae*, but occurred often in *A. pterygocercus*. In a sample of $n = 20$ adults of *A. susanae*: 39 intact leg III tibia included 30/39 spurs present, 9/39 (23%) spurs lost; 38 intact leg IV tibiae included 34/38 spurs present, 4/39 (10%) spurs lost. In contrast, in a sample of $n = 31$ adults of *A. pterygocercus*: 60 intact leg III tibiae included 15/60 spurs present, 45/60 (75%) spurs lost; 60 intact leg IV tibiae included 36/60 spurs present, 24/60 (40%) spurs lost. The much higher frequency of degeneration or loss of tibial spurs in *A. pterygocercus* correlates to the ultrapsammophile habit of this species, and we suggest that it represents a derived character state.

DISCUSSION

Of the two species of *Apistobuthus*, *A. susanae* appears to be the more plesiomorphic, with shorter, more robust pedipalps and legs, and shorter ungues. These features make it better adapted for a fossorial existence on more stable, compacted sandy soils around the Tigris-Euphrates River delta. Contrasting features of *A. pterygocercus* appear to be apomorphic conditions, some of them associated with life on shifting sands of the Rub' al-Khali. Ancestral *Apistobuthus* scorpions might antedate formation of the Rub' al-Khali. They could have originally evolved on soft alluvial soils of the Tigris-Euphrates drainage, possibly sharing a common ancestor with the fossorial genus *Odontobuthus* Vachon 1950 (Vachon 1960). Genesis of the Rub' al-Khali dunes is thought to be linked to late Pleistocene (< 800 ka BP) high–latitude glaciations that caused reductions in sea level, exposing marine sediments to deflation by strong winds. During these periods of aridity, the Persian Gulf separating Iran from Arabia was dry, and northern trade winds (Shamal), intensified by temperature gradients and high-pressure cells, drove the formation of extensive dune systems on the Arabian peninsula (Glennie 1996). Active dune formation may have also proceeded during less windy, wetter interglacial periods, with local erosion of mountains yielding alluvial deposits that provided additional sources of sand. The complex, extended chronology of the Rub' al-Khali dunes would have provided many opportunities for adaptive radiation of *Apistobuthus* into sands of the Arabian Peninsula, but it is unclear when this occurred. The most recent time window may have been during the last glacial maximum (~ 20 ka BP) when a dune-adapted *A. pterygocercus* could have been derived by rapid stenotopic speciation (Prendini 2001a) from a fluvial-adapted population residing along a Tigris-Euphrates River that flowed through a dry Gulf out to the Strait of Hormuz. Subsequent post-glacial marine transgression of the Persian Gulf would have exerted an isolating influence that accelerated speciation of the ultrapsammophilous species.

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On the endemic Sri Lankan genus *Pettalus* (Opiliones, Cyphophthalmi, Pettalidae) with a description of a new species and a discussion of its diversity

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Abstract. A new species of Cyphophthalmi (Opiliones) belonging to the Sri Lankan endemic genus *Pettalus* is described and illustrated. Represented in a recent phylogeny of the family Pettalidae, this species was designated *Pettalus* cf. *brevicauda*, but subsequent examination of its morphology and of the type material of *P. brevicauda* indicates that it is a separate species. Characterization of male genitalia and SEM illustrations are included. Information on other morphospecies recently collected in Sri Lanka indicates that the number of species on the island is higher than previously thought.

Keywords: Gondwana, *Pettalus thwaitesi*, Sri Lanka

A recent phylogenetic study of Pettalidae Shear, 1980 labeled this family of Cyphophthalmi (Arachnida, Opiliones) a "new model Gondwanan taxon," due to its remarkable distribution on nearly all landmasses of temperate Gondwanan origin (Boyer & Giribet 2007). Currently, Pettalidae is the most diverse family within Cyphophthalmi with respect to both numbers of described genera and species. The pettalid genera of New Zealand in particular have received much attention in taxonomic and biogeographical studies (Boyer & Giribet 2003; Boyer et al. 2007a, 2007b). It is therefore ironic that the type genus and namesake of the family Pettalidae is arguably the most enigmatic among Cyphophthalmi. For over a century, only two species—the first originally assigned to the genus *Cyphophthalmus*—were formally recognized: *Pettalus cimiciformis* (O. Pickard-Cambridge 1875) and *P. brevicauda* Pocock 1897. The former species was described from a single male specimen, collected in Pundaluoya, and the latter from an adult male and a juvenile male, collected in an unspecified locality in "Ceylon" (specimens deposited at The Natural History Museum, London). All three specimens, collected in the nineteenth century, feature a peculiar modification of the terminal opisthosomal tergites that form the "tail" characteristic of male *Pettalus*. These specimens have been recently illustrated and discussed (Giribet 2008).

Subsequent to the original descriptions (O. Pickard-Cambridge 1875; Pocock 1897), Hansen & Sørensen (1904) undertook a redescription of the anatomy of the specimens for their monograph. However, the redescriptions of Hansen & Sørensen (1904) conflict significantly with the original descriptions, possibly because the two species were confused for each other during redescription and one of the specimens illustrated by Hansen & Sørensen (1904) does not coincide with any of the three specimens reported by Pickard-Cambridge or Pocock (see Giribet 2008). Study of the specimens of *P. cimiciformis* was not resumed until two recent cladistic analyses of the cyphophthalmid genera (Giribet & Boyer 2002) and specifically of the family Pettalidae (Giribet 2003). These specimens are referred to erroneously as *P. brevicauda* by Giribet (2003; see also Sharma & Giribet 2006) following the redescription by Hansen & Sørensen (1904), as discussed by Giribet (2008).

Following a field expedition to Sri Lanka in 2004, specifically to collect *Pettalus*, researchers formally described a third species (*P. lampetides* Sharma & Giribet 2006) from an older collection of 75 *Pettalus* specimens consisting of eight morphospecies (specimens collected by Claude Besuchet and Ivan Löbl in 1970). These are currently deposited at the Muséum d'histoire naturelle, Geneva. Although *P. lampetides* was not found during the 2004 field expedition, the description included the first published SEM images and illustrations of *Pettalus* genitalia. Moreover, the presence of eyes in Pettalidae was observed and illustrated for the first time in the course of the *P. lampetides* description, which fundamentally changed the understanding of eye evolution in Cyphophthalmi (Sharma & Giribet 2006; see also Boyer & Giribet 2007).

The 2004 field expedition resulted in the collection of an additional six undescribed species of *Pettalus*. Due to its superficial resemblance to the holotype of *P. brevicauda* and to its geographical location, one of these was designated as *P.* cf. *brevicauda* and was listed in this manner in two studies: a biogeographical analysis of Pettalidae distribution (Boyer & Giribet 2007) and a broader phylogenetic analysis of the suborder Cyphophthalmi (Boyer et al. 2007b), in addition to a recently published book on Opiliones (Pinto-da-Rocha et al. 2007: fig. 2.1a). This species is also currently being used for sperm ultrastructure and eye ultrastructure studies in G. Alberti's laboratory in Greifswald. However, recent examination of these specimens has indicated that *P.* cf. *brevicauda* is a separate species from *P. brevicauda* in spite of their superficial similarity.

The inclusion of the molecular sequence data of specimens formerly designated *Pettalus* cf. *brevicauda* in multiple published studies, as well as the ongoing ultrastructural studies of sperm and eye anatomy, has made the formal description of this species imperative. Moreover, the significance of Sri Lanka in biogeographical studies of Pettalidae distribution makes the study of *Pettalus* all the more necessary.

METHODS

Abbreviations.—Examined specimens have been deposited in the following institutions: BMNH = The Natural History

Museum, London (UK); MCZ = Museum of Comparative Zoology, Harvard University, Cambridge (USA); MHNG = Muséum d'histoire naturelle, Ville de Genève (Switzerland); MUP = Museum of the University of Peradeniya, Central Province (Sri Lanka).

Three male and three female specimens were examined with a Scanning Electron Microscope (SEM) FEI Quanta 200. The holotype and a female paratype were photographed in dorsal, ventral, and lateral positions using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (from 10 to 15) was taken at different focal planes and assembled with the dedicated software package Auto-Montage Pro Version 5.00.0271 by Syncroscopy. The spermatopositor of a male paratype was examined with a compound microscope with Nomarski Interference Contrast optics, and measured with an ocular micrometer. All measurements are given in millimeters unless otherwise indicated. Nomenclature on cuticular ornamentation follows Murphree (1988).

Specimens previously used for DNA extraction are indicated as such among the type material. Molecular sequence data obtained from these specimens are utilized by Boyer et al. (2007b) and Boyer & Giribet (2007). DNA extraction comprised a non-destructive protocol described in Boyer et al. (2005).

Material for comparison consisted of (1) type specimens of *Pettalus lampetides* (MHNG), Sri Lanka, Diyaluma Falls; (2) holotype of *Pettalus brevicauda* (BMNH), Sri Lanka (locality not specified); and (3) holotype of *Pettalus cimiciformis* (BMNH), Sri Lanka, Punduluoya.

TAXONOMY

Family Pettalidae Shear 1980

Type genus.—*Pettalus* Thorell 1876.

Genus *Pettalus* Thorell 1876

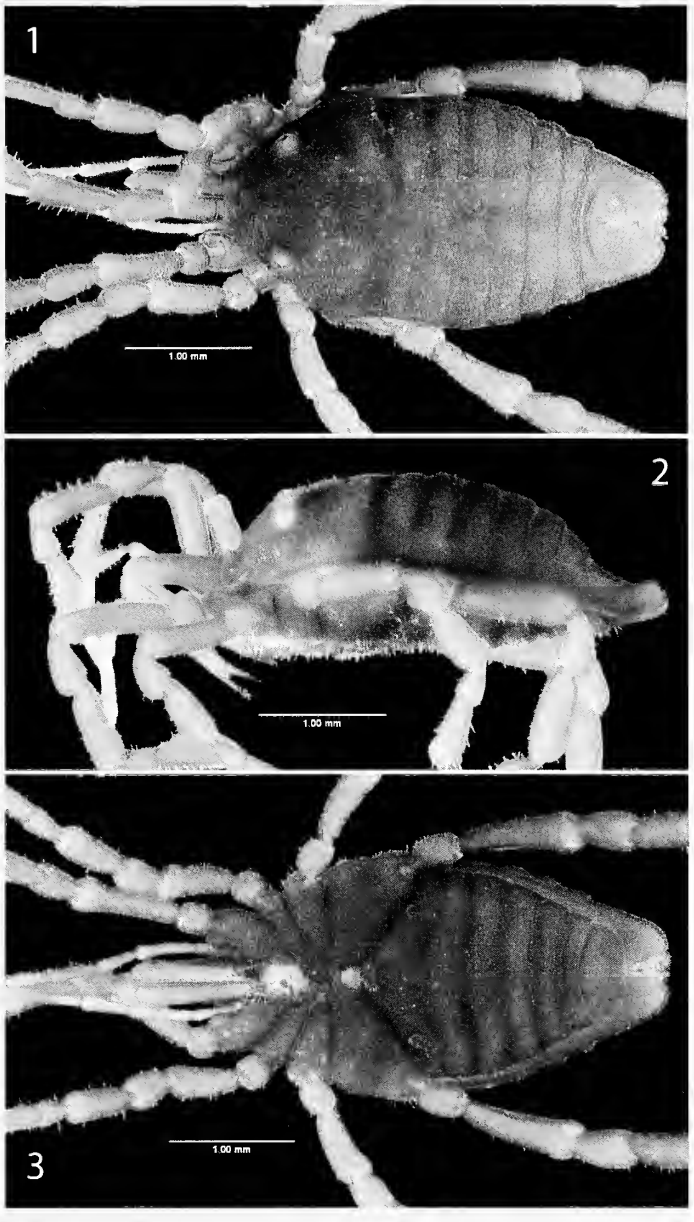
Pettalus Thorell 1876:469.

Type species.—*Cyphophthalmus cimiciformis* O. Pickard-Cambridge 1875, by monotypy.

Diagnosis.—Small to medium-sized Cyphophthalmi with distinct bilobed opisthosomal tergite in males, forming characteristic "tail." Eyes with a distinct lens present at the base of the ozophore. Chelicera slightly protruding, proximal article with dorsal and ventral crest, and dual cheliceral dentition. Palpal trochanter without ventral process. Lamelliform adenostyle, swollen at the base, in most proximal region of tarsus IV. Spiracles in the shape of an open circle, nearly C-shaped. Males and females lacking anal glands and modifications thereof. Spermatopositor short, with two movable fingers in gonopore complex, long dorsal microtrichia with bases arranged in a "V" and not fused, and short apical and ventral microtrichia. Ovipositor composed of two apical lobes, each bearing several setae, a long terminal seta, and a sensitive process with a multi-branched seta.

Pettalus thwaitesi new species
(Figs. 1–28)

Pettalus cf. *brevicauda* Boyer et al. 2007b:2070–2085
Pettalus cf. *brevicauda* Boyer & Giribet 2007:337–361



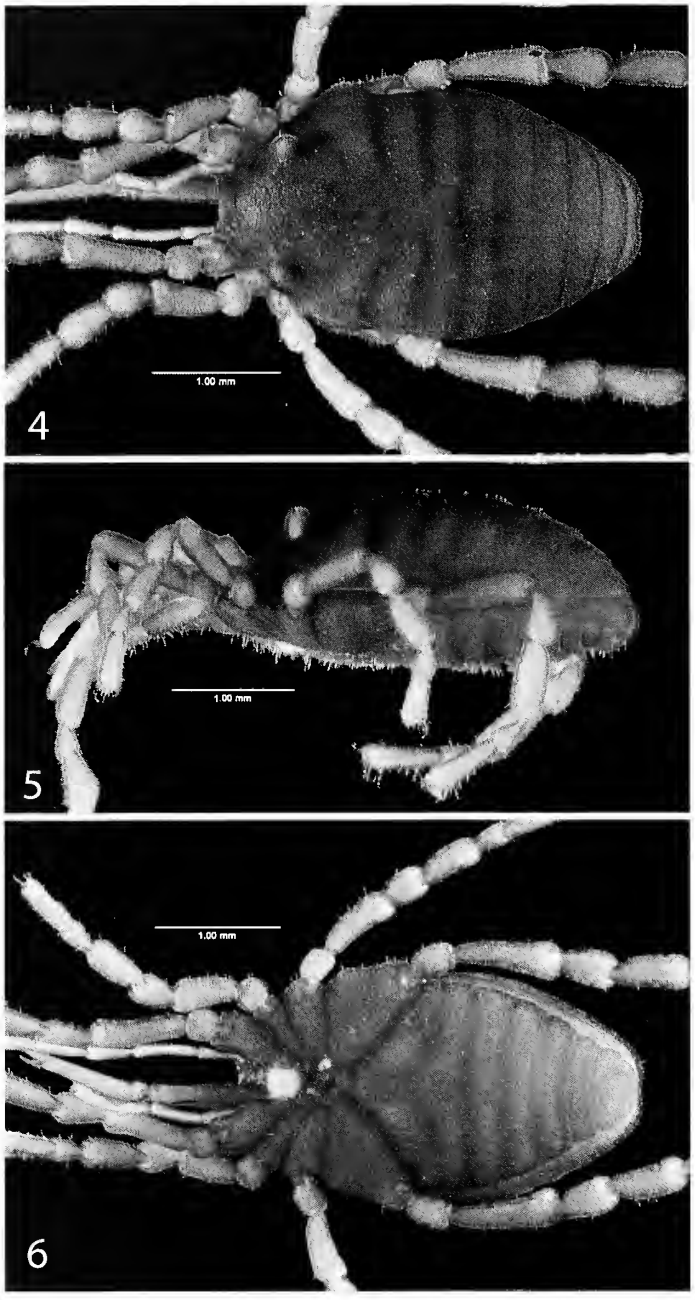
Figures 1–3.—*Pettalus thwaitesi* sp. nov., male holotype (MCZ 78875): 1. Dorsal view; 2. Lateral view; 3. Ventral view.

Pettalus cf. *brevicauda* Shultz & Pinto-da-Rocha 2007:16, fig. 2.1a

Type material.—*Holotype:* SRI LANKA: *Central Province*: ♂, Peradeniya Botanical Gardens (7°15′54″N, 80°35′39″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ 78875, ex MCZ DNA101227).

Paratypes: SRI LANKA: *Central Province*: 4 ♂ (1 dissected for genitalia, 1 used for DNA extraction), 3 ♀, same collecting data as holotype (MCZ 78876, ex MCZ DNA101227); 2 ♂, 1 ♀ same collecting data as holotype (MCZ 78877, 78878, 78879, mounted on SEM stubs); 1 ♂, 1 ♀, same collecting data as holotype (MUP, ex MCZ DNA101227); 1 ♀, Peradeniya Botanical Gardens (7°16′21″N, 80°35′36″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ 78880, ex MCZ DNA101226, mounted on SEM stubs).

Other material studied: SRI LANKA: *Central Province*: 1 ♂ juvenile, same collecting data as holotype (MCZ



Figures 4–6.—*Pettalus thwaitesi* sp. nov., female paratype (MCZ 78876): 4. Dorsal view; 5. Lateral view; 6. Ventral view.

DNA101227); 2 ♂, 2 ♀, Peradeniya Botanical Gardens (7°16′21″N, 80°35′36″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101223); 4 ♂, Peradeniya Botanical Gardens (7°16′21″N, 80°35′36″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101224, preserved for future RNA extraction); 2 juveniles, Peradeniya Botanical Gardens (7°16′21″N, 80°35′36″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101225); 4 ♂ (1 used for DNA extraction), 15 ♀, 6 juveniles, Peradeniya Botanical Gardens (7°16′21″N, 80°35′36″E), 17 June 2004, S.L. Boyer, G. Giribet, I. Karunarathna and P. Sharma (MCZ DNA101226); 2 ♂, 2 ♀, Peradeniya, 19 January 1976, C. Besuchet and I. Löbl (MHNG, 1 ♂, 1 ♀ mounted on SEM stubs).

Etymology.—The specific epithet refers to George H.K. Thwaites, director of the Peradeniya Botanical Gardens in the nineteenth century, who sent the first *Pettalus* specimen to O. Pickard-Cambridge for the description of *P. cimiciformis*.

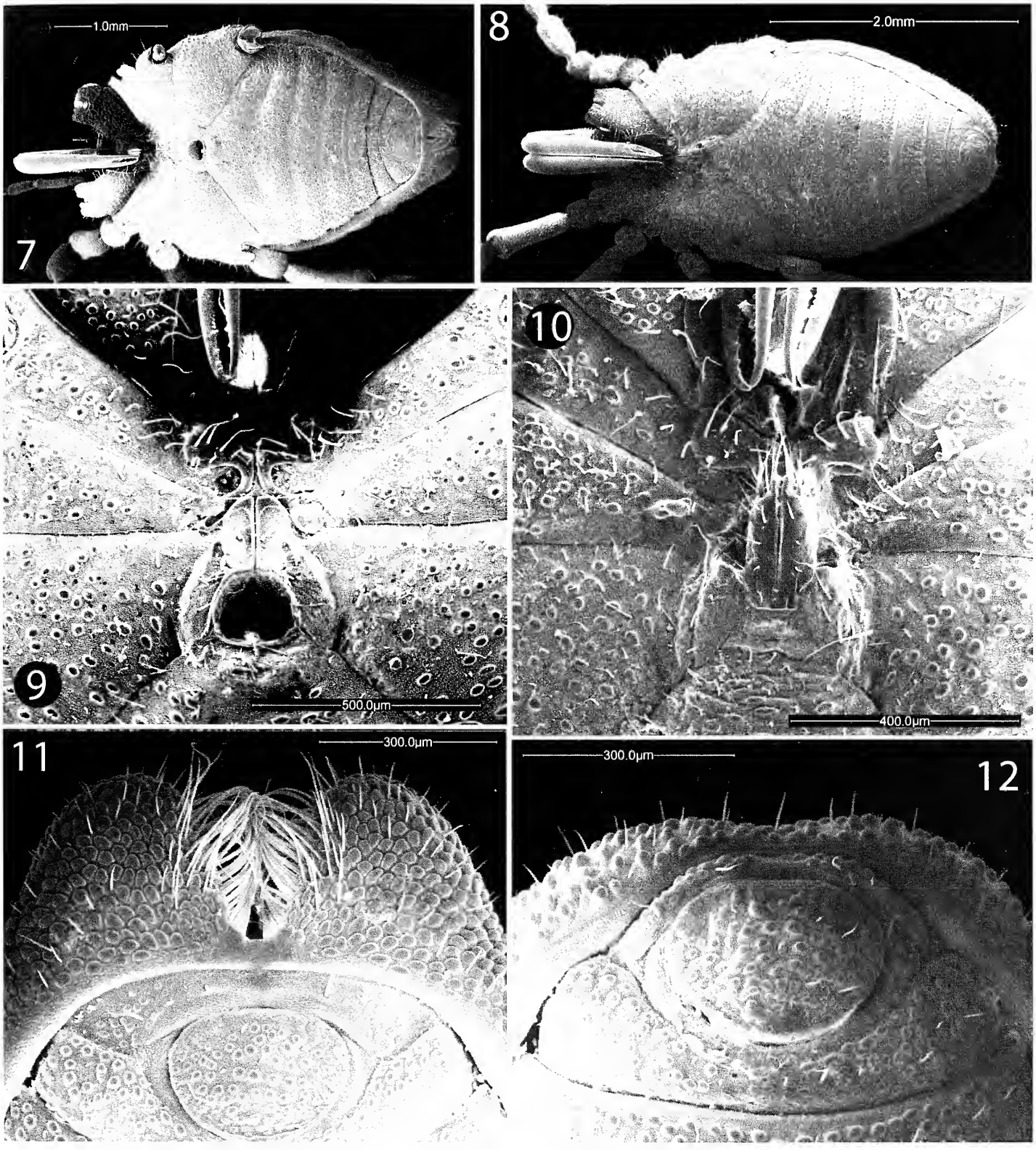
Diagnosis.—Medium-sized pettalid with distinct bilobed opisthosomal tergite in males (Figs. 1–3, 7, 11), slightly bilobed in females (Figs. 4, 8, 12). Ozophores of type 3 (Figs. 1, 4). Eyes present, incorporated at the base of the ozophore, with a distinct lens (Figs. 2, 5). Chelicera slightly protruding (Figs. 1, 2), proximal article with dorsal and ventral crest (Fig. 13), and dual cheliceral dentition (Fig. 14). Palpal trochanter without ventral process (Fig. 16). First and second coxae of walking legs free, third coxae fused to fourth. Adenostyle lamelliform, swollen at its base, in most proximal region of tarsus IV (Fig. 25). Spiracles in the shape of an open circle, nearly C-shaped (Fig. 15). Sternites 8 and 9 and tergite IX free, not forming a corona analis (Figs. 11, 12). Male and female lacking anal glands and modifications thereof. Spermatopositor short, of microtrichal formula 6-6-8, with two movable fingers in gonopore complex (Figs. 27–29).

Description.—Total length of male holotype (female paratype MCZ 78876 in parentheses) 3.58 (3.47), width across ozopores 1.04 (1.15), greatest width 1.94 (2.02), equally wide on widest part of prosoma and on second abdominal segment (Fig. 1); length-width ratio 1.85 (1.72).

Body orange to reddish-brown (when preserved in ethanol) depending on incidence of light. Body almost entirely covered by a dense tuberculate-granulate microstructure. Anterior portion of prosoma tapering towards the anterior margin where the chelicerae insert (Figs. 1, 4). Eyes present (Figs. 2, 5). Ozophores conical, of type 3 of Juberthie (1970; see a redefinition of the types of ozophores in Giribet 2003) (Figs. 1, 2, 4, 5). Transverse opisthosomal sulci conspicuous (Figs. 1, 4). Mid-dorsal longitudinal opisthosomal sulcus absent (Figs. 1, 4). Posterior end of the opisthosomal region clearly bilobed in males as a result of an extension of tergite IX, which tapers, forming the characteristic "tail" of the genus (Figs. 1–3, 7, 11); tergites VI to VIII clearly concave (Fig. 2). Dorsal and ventrolateral parts of tergite IX covered with a high concentration of setae (scopulae) (Figs. 1, 3, 11). Female posterior opisthosomal region without clear modifications, although slightly bilobed (Figs. 6, 12).

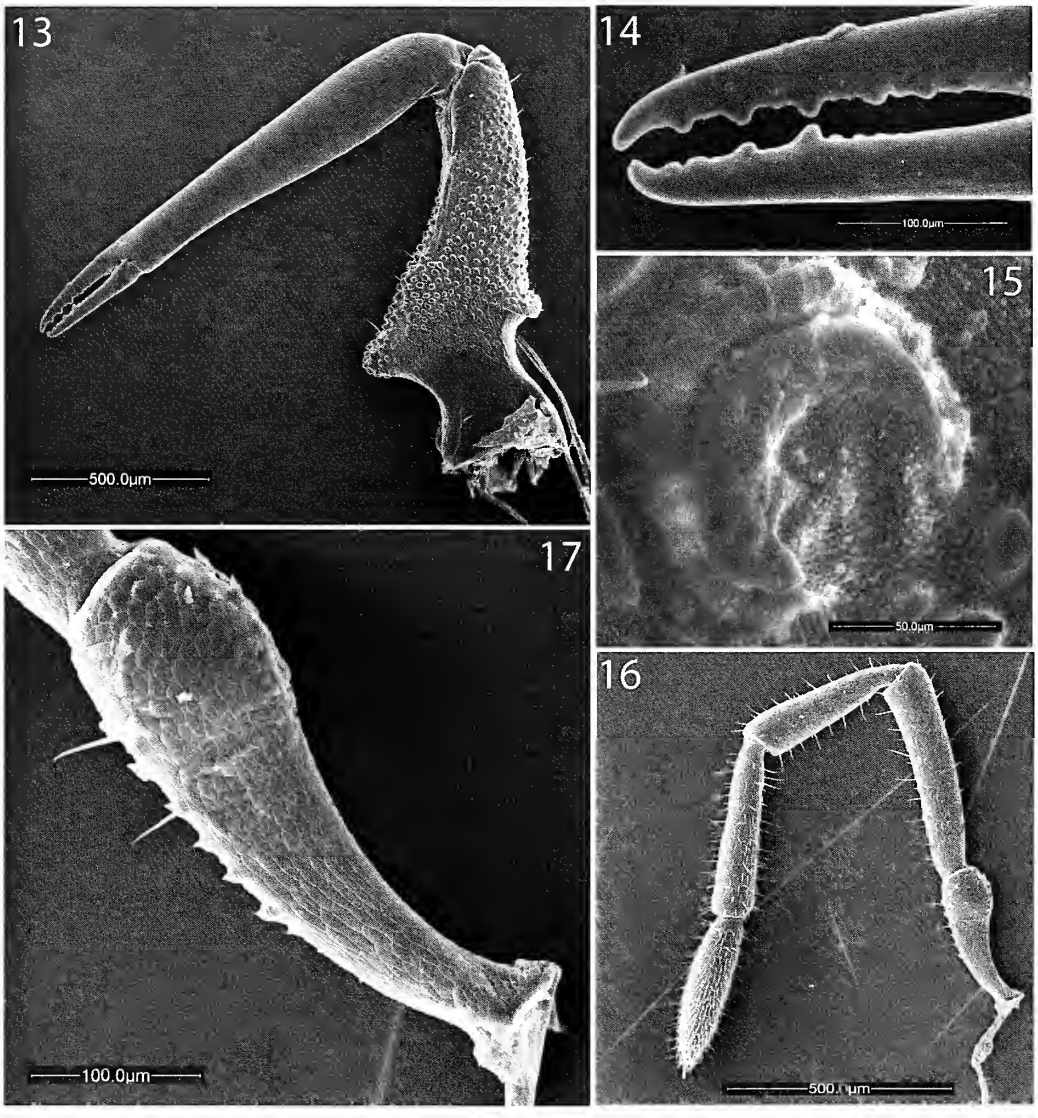
Coxae of legs I and II movable, coxae of legs III and IV fused (Figs. 9, 10). Ventral prosomal complex of male with coxae of legs II and IV meeting in the midline, but coxae I and III not so (Fig. 9). Pore of coxal gland opening between coxae III and IV (Fig. 9). Sternum absent. Gonostome subsemicircular, approximately as long as wide; lateral walls formed by elevated endites of coxae IV. Ventral prosomal complex of female with only coxae II meeting in the midline. Spiracles in the form of an open circle, although almost C-shaped (Fig. 15), opening towards the postero-lateral side. Sternal opisthosomal glands absent. Sternites 8 and 9 and tergite IX free in males and females, not forming a corona analis (Figs. 11, 12). Relative position of sternite 9 and tergite IX of pettalid type, sensu Giribet & Boyer (2002), where the sternite is embedded by the tergite (Figs. 11, 12). Anal plate without modifications, in ventral position in males and females. Anal gland pores absent (Figs. 11, 12).

Chelicerae (Fig. 13) of protruding type, with the dorsal crest clearly visible from above (Fig. 1); relatively slender; with few



Figures 7–12.—*Pettalus thwaitesi* sp. nov.: 7. Ventral view of male paratype; 8. Ventral view of female paratype; 9. Sternal region of male paratype; 10. Sternal region of female paratype; 11. Anal region of male paratype; 12. Anal region of female paratype.

setae. Granulation restricted to the proximal article covering almost the entire surface, but not the most distal portion. Proximal article of female paratype (MCZ 78876) 1.07 long, 0.46 deep, with conspicuous dorsal crest that extends ventrally but without forming a ventral process, and single posterior ventral process. Second article 1.32 long, 0.19 deep, subcylindrical, its widest portion towards the first third of its length; dentition irregular. Distal article 0.27 long, 0.06 deep, with the two types of dentition typical of pettalids (Fig. 14).



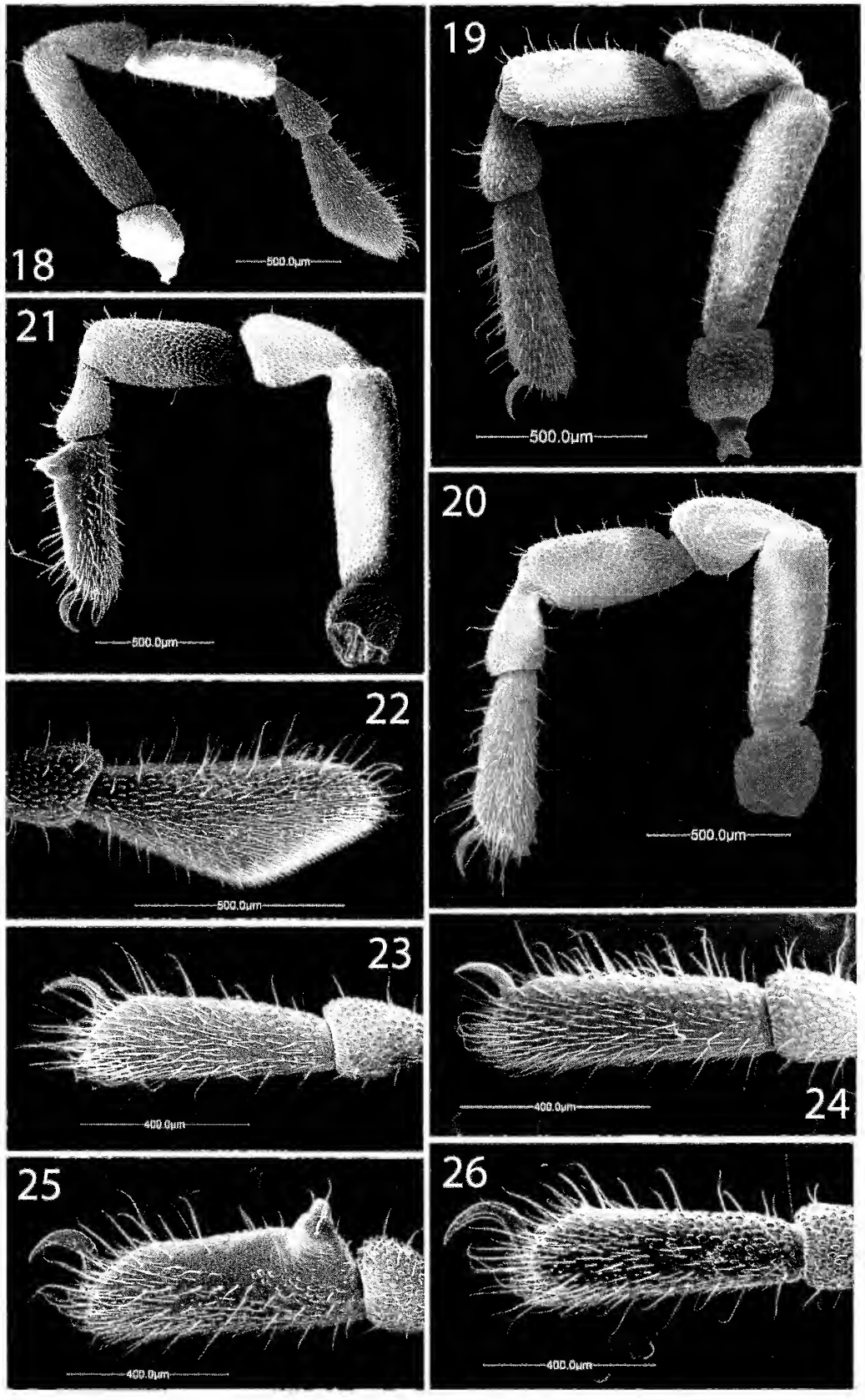
Figures 13–17.—*Pettalus thwaitesi* sp. nov.: 13. External view of left chelicerae of male paratype; 14, Detail of dentition of distal cheliceral segment; 15. Spiracle of male paratype; 16. Left palp of male paratype; 17. Trochanter of male paratype.

Palp (Fig. 16) without ventral process in trochanter (Fig. 17); without conspicuous modifications. Length/width (length-width ratio in parentheses) of palpal articles from trochanter to tarsus of holotype [of female paratype in square brackets]: 0.25/0.11 (2.27) [0.26/0.11 (2.36)]; 0.57/0.11 (5.18) [0.55/0.11 (5.00)]; 0.38/0.11 (3.45) [0.40/0.11 (3.63)]; 0.47/0.10 (4.70) [0.45/0.09 (5.00)]; 0.38/0.08 (4.75) [0.41/0.09 (4.56)]; total length 2.05 [2.07].

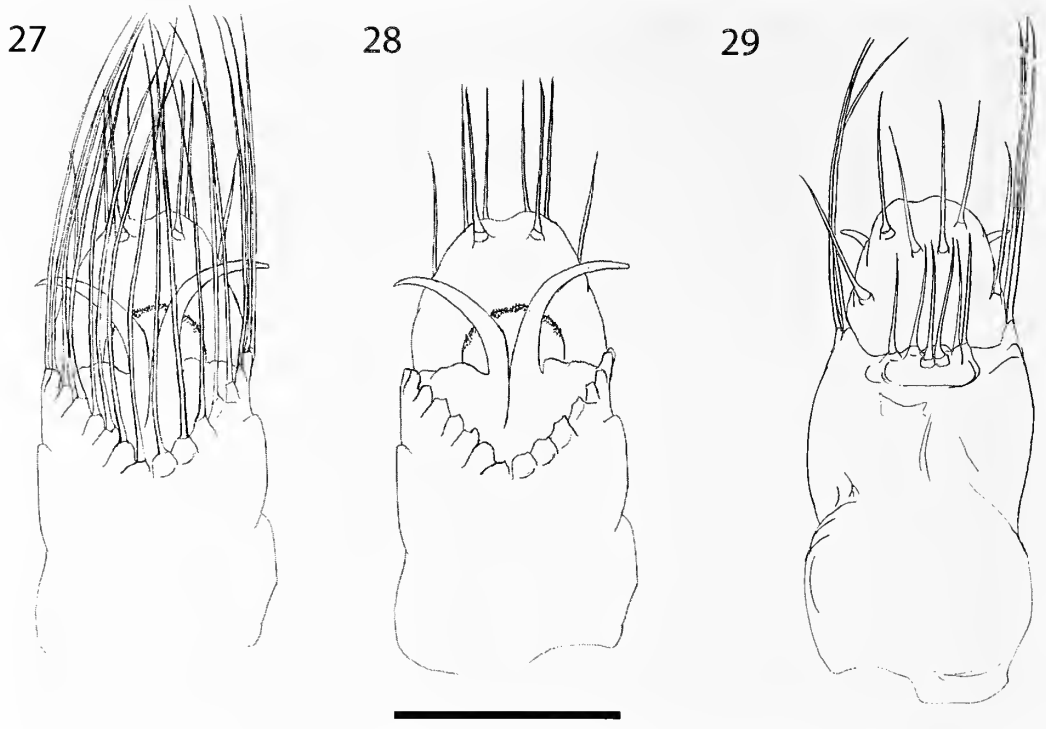
Legs (Figs. 18–26) with all claws smooth, lacking dentition or lateral pegs. Surfaces of all trochanters, femurs, patellae, tibiae and metatarsi granulated Figs. 18–21). Granulation of all tarsi concentrating in the proximal and dorsal side (Figs. 22–24, 26); in the case of the male tarsus IV, granulation concentrating in the proximal side, below the adenostyle (Fig. 25). Tarsus I with a distinct solea (Figs. 18, 22). Tarsus IV of males not divided, carrying a lamelliform adenostyle, swollen at its base, in most proximal region of tarsus (Figs. 21, 25). Adenostyle typically folded or bent away from the vertical axis (Fig. 25). Tarsus IV of female without modifications (Fig. 26).

Spermatopositor (Figs. 27–29) short, typical of pettalids. Microtrichal formula 6-6-8 (one spermatopositor studied). Dorsal side with a group of eight long microtrichia on each side, with bases arranged in a "V" and not fused. Rounded distal margin with six apical microtrichia, and six short microtrichia adjacent ventrally. Gonopore complex with two distinct movable fingers in the shape of curved hooks.

Leg measurements.—Male holotype (MCZ 78875) in mm, length/width (length/width ratio in parentheses): Leg I: trochanter 0.28/0.26 (1.08), femur 0.94/0.24 (3.92), patella 0.48/0.26 (1.85), tibia 0.66/0.23 (2.87), metatarsus 0.35/0.20 (1.75), tarsus 0.69/0.30 (2.30), total 3.40. Leg II: trochanter 0.23/0.23 (1.00), femur 0.71/0.22 (3.23), patella 0.45/0.25 (1.80), tibia 0.54/0.24 (2.25), metatarsus 0.32/0.18 (1.78), tarsus 0.59/0.19 (3.11), total 2.84. Leg III: trochanter 0.26/0.25 (1.04), femur 0.68/0.27 (2.52), patella 0.45/0.26 (1.73), tibia 0.42/0.22 (1.91), metatarsus 0.38/0.20 (1.90), tarsus 0.57/0.20 (2.85), total 2.76. Leg IV: trochanter 0.31/0.24 (1.29), femur 0.99/0.32 (3.09), patella 0.59/0.32 (1.84), tibia 0.74/0.32 (2.31), metatarsus 0.39/0.25 (1.56) , tarsus 0.69/0.22 (3.4), total 3.71.



Figures 18–26.—*Pettalus thwaitesi* sp. nov.: 18. Male right leg I; 19. Male left leg II; 20. Male left leg III; 21. Male left leg IV; 22. Detail of male right tarsus I; 23. Detail of male left tarsus II; 24. Detail of male left tarsus III; 25. Detail of male left tarsus IV; 26. Detail of female left tarsus IV.



Figures 27–29.—*Pettalus thwaitesi* sp. nov.: 27. Total spermatopositor, dorsal view; 28. Dorsal view showing apical microtrichia and movable fingers; 29. Ventral view. Scale bar = 200 μm.

Female paratype (MCZ 78876) in mm, length/width (length/width ratio in parentheses): Leg I: trochanter 0.28/0.24 (1.17), femur 0.89/0.27 (3.30), patella 0.45/0.26 (1.73), tibia 0.59/0.22 (2.68), metatarsus 0.35/0.18 (1.94), tarsus 0.61/0.29 (2.10), total 3.17. Leg II: trochanter 0.26/0.22 (1.18), femur 0.71/0.27 (2.63), patella 0.42/0.26 (1.62), tibia 0.48/0.25 (1.92), metatarsus 0.35/0.19 (1.84), tarsus 0.52/0.17 (3.06), total 2.74. Leg III: trochanter 0.25/0.24 (1.04), femur 0.75/0.29 (2.59), patella 0.45/0.26 (1.73), tibia 0.49/0.27 (1.81), metatarsus 0.37/0.20 (1.85), tarsus 0.51/0.18 (2.83), total 2.82. Leg IV: trochanter 0.31/0.24 (1.29), femur 0.89/0.30 (2.97), patella 0.51/0.31 (1.65), tibia 0.61/0.30 (2.03), metatarsus 0.38/0.21 (1.81), tarsus 0.62/0.19 (3.26), total 3.32.

Variation.—Range of measurements in males (n = 4) and females (n = 5; in parentheses): Body length 3.38–3.58 (3.38–3.60), maximum (and anterior) width 1.80–1.85 (1.96–2.20).

Distribution.—Known only from the type locality.

Remarks.—*Pettalus thwaitesi* is readily distinguishable from *P. lampetides* by its greater size and the tapering of its opisthosomal tergites. The posterior end of *P. thwaitesi* tapers gradually, whereas that of *P. lampetides* tapers more abruptly in the middle of the opisthosoma. Moreover, spermatopositor morphology, specifically the number of short ventral microtrichia (six in *P. thwaitesi*, two in *P. lampetides*) readily distinguishes the two. *P. thwaitesi* is smaller than *P. cimiciformis* and has a proportionally smaller upturned "tail." Unlike both *P. cimiciformis* and *P. brevicauda*, *P. thwaitesi* has "protruding chelicers" (sensu Giribet 2003) that do not articulate with the anterior margin of the carapace. Phylogenetically, *P. thwaitesi* is sister to an undescribed species collected from the Hakgala Botanical Gardens, also from the Central Province (Boyer & Giribet 2007).

DISCUSSION

Pettalus thwaitesi clearly belongs to the genus *Pettalus* on the basis of the apomorphic modification of the terminal opisthosomal tergites forming a "tail" shared by the previously described species of *Pettalus*. In addition, the typically double cheliceral dentition, ozophore type, and male genitalia are in accordance with traditionally defined pettalid synapomorphies. The monophyly of *Pettalus* and the inclusion of *Pettalus thwaitesi* have also been demonstrated in multiple molecular phylogenies (Boyer & Giribet 2007; Boyer et al. 2007b).

The description of a second *Pettalus* spermatopositor in the present study recapitulates the usefulness of genitalic morphology in distinguishing closely related species of Cyphophthalmi. Continued study of *Pettalus* diversity should not overlook the taxonomic worth and evolutionary implications of spermatopositor morphology.

Despite the paucity of described *Pettalus* species, at least thirteen morphospecies remain available for description and study. These include (1) the seven morphospecies from the 1970 MHNG expedition, (2) the remaining five from the 2004 MCZ expedition, and (3) one other species collected by S. Mahunka & L. Mahunka-Papp, deposited at the Hungarian Natural History Museum (Budapest). The distribution of these species in a relatively small area suggests significant diversity of cyphophthalmid fauna in Sri Lanka. Due to the small size and leaf-litter habitat of most cyphophthalmid species, it is probable that additional species will be discovered on the island.

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Characterization of the green iridescence on the chelicerae of the tube web spider, *Segestria florentina* (Rossi 1790) (Araneae, Segestriidae)

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Abstract. *Segestria florentina* (Rossi 1790) (Segestriidae) displays iridescent green coloration on the paturons of the chelicerae. This was confirmed by reflectance measurements, which gave a spectral peak at 505 nm. Scanning electron microscopy did not identify cuticular surface scales or sculpturing, suggesting that the cause of the iridescence was subsurface. Transmission electron microscopy revealed 86 alternate dark and light layers in the exocuticle, the mean dimensions of which were 126 nm ± 28 nm and 88 nm ± 55 nm respectively. The identity of each layer was initially unclear. However, by using a combination of materials with different refractive indices in calculations of theoretical reflectance spectra, we concluded that they were most likely to be composed of chitin and air, since a peak of 480 nm was obtained, which most closely matched that which was recorded. The function of the green color is not clear, since *S. florentina* has relatively poor vision and relies predominantly on vibratory and acoustic signals. The study provides useful information relevant to research into the evolution of structural colors in spiders and, more generally, in nature.

Keywords: Structural color, photonic, multilayer reflector

Structural colors are the result of the interaction of light with physical structures, termed photonic crystals, which are in or on the surface of a substratum. They have been identified from a diverse range of taxa, most notably butterflies (Ghiradella 1991; Kinoshita et al. 2002; Biró et al. 2003; Vukusic et al. 2004; Ingram 2008) and birds (Prum et al. 1999; Zi et al. 2003; Li et al. 2005; Vigneron et al. 2006), which have long been the focus of photonics research since their structural colors are very obvious. There are, however, many more instances of structural coloration, which are yet to be described – for example, in spiders. Of the few studies conducted, almost all have concentrated on jumping spiders (Salticidae), as structural colors occur mainly in this family. Multilayer reflectors have been the most commonly occurring photonic crystal, identified from modified setae or cuticular scales (Cutler & Richards 1972; Hill 1979; Holl 1987; Land et al. 2007) and epicuticular surface sculpturing (Parker & Hegedus 2003) on the abdominal and cephalothoracic regions, on which these colors are typically located. Diffraction gratings have also been discovered, individually or in combination with a multilayer reflector (Kochalka 1980; Parker & Hegedus 2003). Here, we extend the literature on spider photonics by describing the structural origin of the green iridescence on the chelicerae of the tube-web spider, *Segestria florentina* (Rossi 1790), using a combination of electron microscopy, spectroscopy and optical modelling. Structural colors have not previously been examined from this haplogyne family. It is therefore hoped that the results will provide useful information, which when considered with those describing iridescence in the highly-derived Salticidae, will contribute to our understanding of the evolution of structural color in spiders.

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Spectral measurements were taken from a specimen of *S. florentina*, which was provided in 70% ethanol by The Natural History Museum (London). A chelicera was dissected from the specimen and illuminated with a halogen source incident at 0° to the surface ("normal incidence"). Reflected light returning along the same illumination pathway ("backscatter") was measured using an Avantes Avaspec 2048/2 spectrometer. The reflection was normalized using a white diffusive standard. Due to the difficulty of measuring spectra from such a small specimen and also the curvature of the sample, a second measurement was taken from the second chelicera of the same individual, for confirmation. A 2 mm^2 section of the dorsal paturon was dissected from one sample and glued with Araldite^{TM} to a glass slide. This provided a sufficiently flat surface from which to measure reflectance spectra with a Roper Spectral-DV^{TM} spectrometer mounted on an Olympus microscope, equipped with a rotating slide holder. This experimental set-up enabled spectra to be recorded from multiple points on the specimen. Data were then collated using Mélange image processing software. The specimen was illuminated, as before, with a halogen source at close to normal incidence and backscattered light (375–700 nm) was collected from a narrow cone around the same angle. Spectra were acquired at 20× magnification.

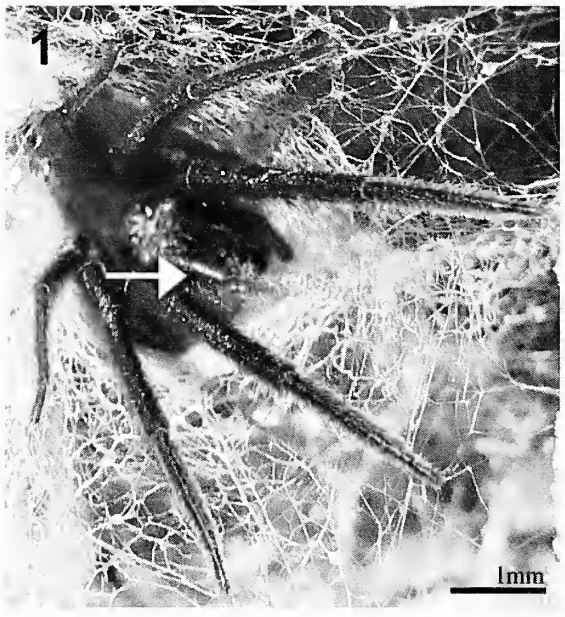
Previous studies have identified cuticular surface and subsurface structures as the cause of interference colors in spiders. A sample was therefore prepared for scanning and transmission electron microscopy (SEM and TEM respectively). For the former, a chelicera was transferred from 70% ethanol to 70% acetone and then dehydrated through a graded acetone series before being critical point dried. It was then coated with gold, mounted on a metal stub using Araldite^{TM} and viewed with a Philips XL30 Field Emission SEM. Images were recorded digitally. A further sample was prepared for TEM, which was immersed in 70% acetone and then

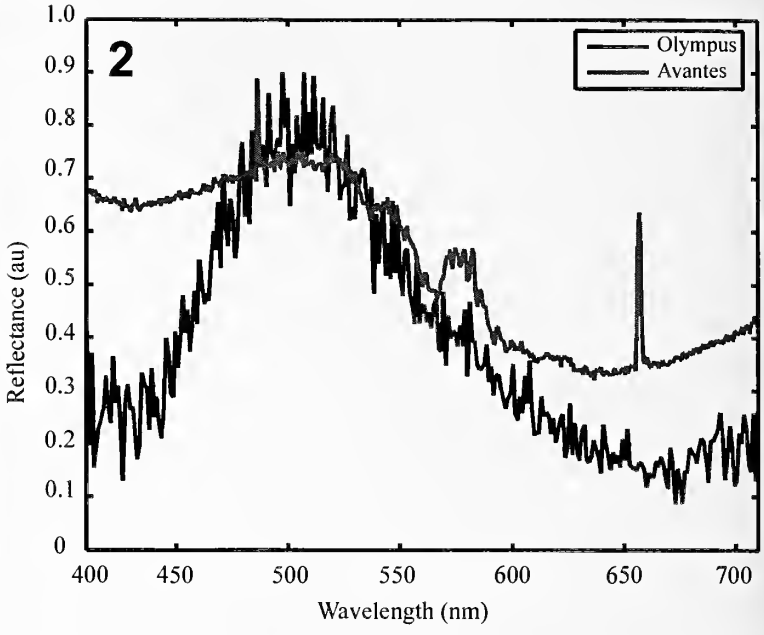
progressively dehydrated through increasingly concentrated acetone to 100% dried acetone. Samples remained here for 48 h before beginning the resin infiltration process using TAAB medium grade resin. Previous experience (Kennaway et al. 2004) has shown that the most important factor in successfully infiltrating terrestrial arthropods is first to ensure that there is no residual water in the specimens (through extended dehydration times) and secondly to ensure that the resin has penetrated the specimens properly (by use of thinned, or low viscosity resin). The resin infiltration process consisted of immersing the sample in a mixture of resin and acetone and progressively inereasing the concentration of resin in the mixture. This was achieved over four days starting with a mixture of approximately 20% resin, 80% dried absolute aeetone. Each mixture was changed after about 12 h and each step was carried out for 24 h. Finally, the infiltrated sample was placed in a resin-filled, flat-ended BEEM capsule and polymerized for 8 h at 70° C. Sections for TEM were cut at 70–90 nm thickness, collected onto grids and counterstained using alcoholic uranyl acetate and Reynold's lead citrate, prior to examination in a Hitachi H7100 TEM. Images were recorded onto film and then scanned from prints.

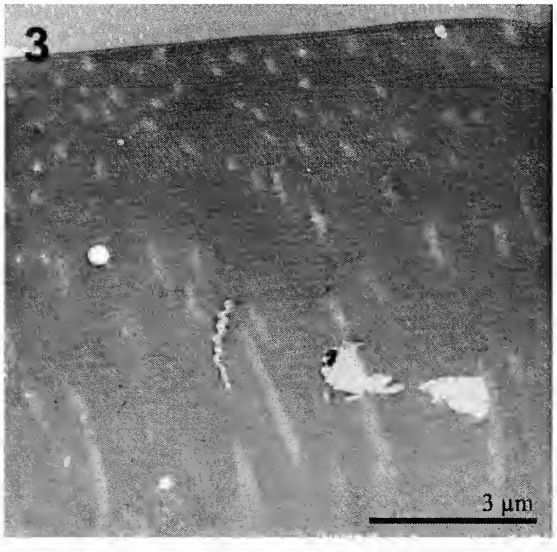
Theoretical reflectance spectra were calculated by the continued-fraction method, which relies on exactly solving Maxwell's equations for an arbitrarily stratified medium (Dereux et al. 1988). In this method, the reflection coefficients for transverse-electric and transverse-magnetic polarized light are expressed in terms of the surface impedances, which take the form of continued fractions. These continued fractions terminate for a finite number of layers deposited onto an infinitely thick substrate (of known refractive index). Their values are determined as soon as the thickness and the refractive index of all the layers are known and the incidence conditions are given. The incidence angle was set to 0° (ineidence medium: air) so that the specular reflection occurred exactly in the backward direction ("backscatter"). Layer thickness values were determined from TEM cross-sectional images and used for calculation. The stratified medium was assumed to be formed by the alternation of low and high density materials (the reason why we chose to model the stack of layers by a periodic multilayer will be explained later on). The precise identity of the two constituent materials was, however, unclear in the absence of data eoncerning the refractive indices of materials comprising spider reflectors. Sinee these values are hard to determine experimentally, we used the results from a number of different approaches: 1) a basic infiltration test (using acetone) for detecting the presence of empty (air-filled) layers (see Parker 2000); 2) previous studies, which have reported spider reflectors from the abdominal and cephalothoracic regions as being comprised of air and chitin layers (Parker & Hegedus 2003; Land et al. 2007); 3) using the aforementioned information, we alternated the refractive indices of possible constituent materials to obtain the best fit between the empirical and theoretical spectra. The refractive index of the organic material was taken to be constant over the whole spectral range. The refractive index of the substrate (beneath the stratified medium) was taken to be equal to that of the bulk organic material. Although the continued-fraction method allowed us to calculate the reflectance for all layers appearing on the TEM images, such a calculation did not lead to a clear peak in the spectrum because variations of the layer thickness across the stack tended to destroy light interference. For this reason, we chose to model the actual structure by a periodic multilayer stack with the same number of layers but constant thicknesses.

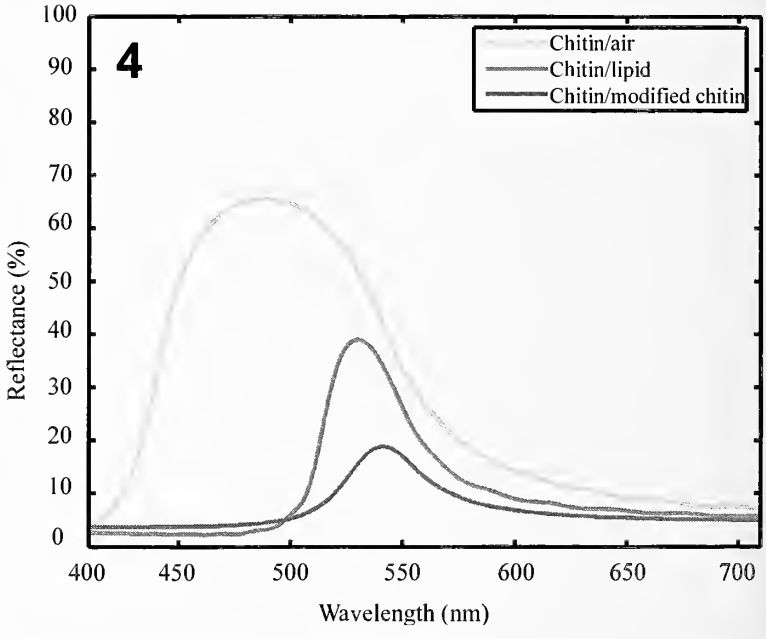
Initial observations of the chelicerae showed that under most angles of illumination and observation, the bright green iridescence originated from the dorsal surface of the paturon (Fig. 1). This was confirmed by the two measured spectra taken from this region, which indicated two similar reflectance peaks around 505 nm (green) (Fig. 2). Scanning electron microscopy revealed that the dorsal surface of the paturon was predominantly smooth, devoid of scales or surface sculpting, suggesting that the origin of the iridescence lay below the cuticular surface. Sections of the paturon were, therefore, examined with the TEM and showed that the exocuticle is composed of an outer region extending 7–8 μm towards the interior, in which around 86 alternate dark and light layers were observed (Fig. 3). Measurements of the thickness of each layer showed that they were highly variable: 126 nm ± 28 nm and 88 nm ± 55 nm, respectively. For this reason, the mean values were used for the theoretical reflectance spectra calculation.

The material of the high density layers was assumed to be chitin, based on previous literature (Richards 1951; Parker & Hegedus 2003). The results of the acetone test showed no color change, suggesting that the less dense layers were not composed of air. Based on this, we modeled spectra using a combination of chitin and a lipid with a refractive index (RI) of 1.46 (Bausch & Lomb), since cuticle contains lipid (Richards 1951). Also chitin and a low RI chitin-based material (n = 1.40) (Bernard & Miller 1968), and finally chitin and air, to give weight to the acetone test. Assuming a refractive index of chitin equal to 1.56 (real part) (Land 1972), the optical path length across a chitin/low density bi-layer at normal incidence is equal to $\delta = (d_{chitin} \times n_{chitin}) + (d_{low} \times n_{low})$, where d_{chitin} and d_{low} are the average actual thicknesses of the chitin layer (126 nm) and low density layer (88 nm), n_{chitin}= 1.56 (chitin) and n_{low}= 1.0 , 1.40 or 1.46 (air, lipid, or low RI chitin-based material) are the refractive indices respectively. The condition of constructive interference upon reflection at normal incidence in a quarter wavelength multilayer stack, $\delta = m \times \lambda/2$, predicts that the Bragg wavelength (m = 1) is located in the visible range: 567 nm (air), 637 nm (lipid) and 648 nm (low RI chitin-based material) from the green end of the spectrum to the red (Fig. 4), suggesting that the low density layers are most likely to be composed of air. The failure of the acetone test to identify air as a constituent is likely due to the fact that the structure is sealed. The reflectance of a stack made of 50 alternating layers of chitin and 1) air 2) modified chitin and 3) lipid was calculated at normal incidence. We chose to consider the first 50 alternating layers (over 86 in total) due to the large fluctuations observed in layer thicknesses. The averaged thickness values of these layers, d_{chitin} = 115 nm and d_{low} = 62, were found to be slightly lower than the ones cited above, leading to a shift of the Bragg wavelengths to shorter wavelengths: 481 nm (air), 530 nm (lipid), and 538 nm (low RI chitin-based material). An imaginary part (i) was added to the refractive index of chitin and modified chitin to take into









Figures 1–4.—*Segestria florentina* (Rossi 1790) (Segestriidae). 1. Frontal view of an adult female, indicating green iridescent chelicera. 2. Reflectance spectra (au - arbitrary units) recorded from the paturon using two types of spectrometer (Avantes / Olympus microscope-mounted). Both illumination and measurement angles were set to 0° (normal incidence) in each case. 3. Scanning electron micrograph of a transverse section through a paturon. 4. Theoretical reflectance spectra (%) from the paturon, by the continued-fraction technique. Incidence and reflection angles set to 0°. Three combinations of materials were used: Chitin/air, chitin/lipid and chitin/modified chitin with the refractive indices set to 1.0 (air), 1.56 (chitin), 1.46 (modified chitin), and 1.40 (lipid).

account optical absorption in the chitin material (n_{chitin} = 1.56 + i × 0.05, n_{low} =1.40 + i × 0.05). This complex refractive index was assumed to be constant across the whole wavelength range (350–710 nm), in a first approximation. The results showed that the best agreement with the measured reflectance spectra was obtained using chitin and air (Fig. 4).

The chelicerae display some of the most striking structural colors found in spiders (Jackson 1982). They are probably most well known from the Salticidae, however, they also occur in the Segestriidae. In both cases, naturalists and scientists have been aware of their existence for some time and yet the cause of the color has remained unexplained. In the current study we chose to examine the iridescent green chelicerae of *S. florentina*, from which the cause of the color was identified as a constructively-interfering multilayer reflector. Studies have identified this type of reflector elsewhere in spiders (Cutler & Richards 1972; Hill 1979; Holl 1987; Parker & Hegedus 2003; Land et al. 2007) and it is emerging as the most common type of photonic crystal in this group, as it is in butterflies (Ingram 2008) and structurally colored animals in general (Parker

2006). This convergently evolved optical structure typically provides an effective method of displaying bright color to conspecifics without attracting the unwanted attention of predators (Parker 1998). However, it is unclear if this is the intended function of the color in *S. florentina*. Unconfirmed reports suggest that the similarly green iridescent chelicerae of the unrelated genus, *Phidippus* (Salticidae), are employed in conspecific (mate) recognition (Irene Lindsey, pers. comm.). Additional evidence for this originates from studies of vision in the related species, *P. regius* Koch 1846, which showed that the eyes have a corresponding peak spectral sensitivity in the green (de Voe 1975). It is unlikely that the chelicerae of *S. florentina* function in mate recognition, since the family is known to have relatively poor vision, relying predominantly on vibratory (Barth 1982) and acoustic signals (Gertsch 1979). To determine the role of the color, behavioral and visual data are required to determine if the green has some adaptive function in signaling.

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Post-reproductive changes in female crab spiders (*Misumena vatia*) exposed to a rich prey source

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Abstract. Life history theory predicts that the intensity of selection will decline as individuals age; thus, adaptive traits should decrease during post-reproductive stages. To test this prediction, I measured several potential fitness variables in adult female crab spiders [*Misumena vatia* (Clerck 1757): Thomisidae]: maximum mass before laying, mass after laying, mass at release into hunting site, carapace width, and days since egg-laying upon A) daily rate of loss in mass after egg-laying while guarding a brood and B) daily rate of gain in mass after release into a rich hunting site. These individuals were members of a normally semelparous population guarding their nests without feeding for 1–26 days past egg-laying. Rate of decline in mass of the spiders slowed significantly over time ($P < 0.01$), and large individuals lost mass relatively faster than smaller ones ($P < 0.05$), but no other tested variables affected their rate of loss in mass. However, none of the above-noted variables significantly affected their rate of gain in mass after release into the hunting site. None of these individuals likely produced a second brood. The scarcity of relationships among variables measured, especially those following release into the rich hunting site, is consistent with these individuals experiencing little or no direct selection for fitness-enhancing traits subsequent to egg-laying. The exceptions noted for the guarding period probably resulted directly from success at an earlier life stage.

Keywords: Dispersal, gain in mass, nest-guarding, semelparity, senescence

Life history theory holds that the expected future reproductive success (reproductive value) of individuals declines with age, with selection consequently weakening over time (Fisher 1930; Williams 1957). This state of affairs likely presents a potent force driving populations toward obligate semelparity (reproducing only once) (Roff 1992; Stearns 1992). Following reproduction, a semelparous individual should experience no further selective pressure favoring subsequent survival or reproduction, constrained only by possible responsibilities to its offspring (egg-guarding, defense of young, etc.) (Packer et al. 1998). Thus, such an individual may exhibit a decrease in adaptive patterns as its responsibilities to its young decrease. Fisher maintained that even factors such as parental care usually remain unimportant relative to the main effects of a single large reproductive effort. According to this argument, parents should expend all available resources on direct reproductive output (gametes) at the expense of parental care. Indeed, some species, such as the often-cited Pacific salmon *Oncorhynchus* spp. (Willson 1997), expend so many of their resources immediately prior to and at reproduction that they die soon afterward.

Facultatively semelparous individuals lie intermediate to obligately semelparous and iteroparous conditions and may provide excellent insights into the question of whether to invest in a single brood or to attempt a second. Facultatively semelparous forms include Condition 1) individuals able to replace an initial brood lost part way through the normal period of care (Schneider et al. 2003; Futami & Akimoto 2005), in which case only a single brood survives; and Condition 2) individuals that usually lack the time to produce a second brood (e.g., a short season), though physiologically capable of doing so (Tallamy & Wood 1986; Morse 1994; Schneider et al. 2003). Given the uncertainty associated with Condition 2, individuals of species that guard their broods may confront the important decision of whether to continue guarding, thereby enhancing the survival of their young (Morse 1988a, 1992) or to gamble that by abandoning their first brood to its own devices so they can successfully rear a second brood.

Crab spiders *Misumena vatia* (Clerck 1757) (Thomisidae) provide a particularly favorable opportunity to investigate the relative advantages of guarding young and producing a second brood. In coastal Maine, USA, *Misumena* lay a single brood under normal field conditions and exhibit an extremely high reproductive effort (Fritz & Morse 1985), yet when supplementally fed so that they overcome severe seasonal time constraints resulting from foraging under unpredictable conditions (Morse & Fritz 1982), they may produce second broods (Morse 1994). Further, they exhibit occasional signs of attempting to produce a second brood under natural circumstances at our study sites (Morse 1994). Although the short season probably prevents them from producing a successful second brood if not supplementary fed, almost half of them abandon their brood before the young emerge from the nest. Some of the individuals that leave their broods hunt voraciously and gain considerable mass if they find a satisfactory hunting site, and occasionally will even build and guard second nests, none of which to date have contained eggs (Morse 1994, unpublished data).

Two factors that should favor production of a second brood are minimizing loss of mass while guarding their eggs (after laying) and, especially, maximizing gain in mass after leaving their eggs. Variables likely to affect these two factors include maximum mass before laying, mass immediately after laying, mass at subsequent release into a foraging site, skeletal body size (carapace width), and number of days guarding after laying.

Here I evaluate the hypothesis that post-reproductive responses (after egg-laying), acting through the variables outlined immediately above, maximize an individual's opportunity to rear a second brood. If second broods are to succeed, I predict that some or all of these five independent variables will differ in ways that allow the spiders to enhance fitness, either by minimizing loss in mass or by maximizing rate of

gain in mass after egg-laying. Earlier work demonstrated that most females retain adequate sperm to fertilize a second brood (Morse 1994), so failure to mate after their first brood should not impede them from producing a fertile second brood.

To test predictions A and B and to evaluate the role of several variables, I measured loss in mass from egg-laying until release into a hunting site. These individuals had no access to food after egg-laying. Although that starvation regime may appear extreme, post-reproductive guarding *Misumena* seldom capture prey since they usually nest where few insects visit (Morse 1987). I then measured the spiders' rate of gain in mass after their release into the rich hunting site.

METHODS

Study site.—I carried out this study in the summers of 2001–2007 at the Darling Marine Center, South Bristol, Lincoln County, Maine (43.57°N, 69.33°W), in a 3.5 ha field containing several forbs that provide hunting sites for the spiders when the flowers are in bloom. I have described this field in detail elsewhere (Morse 2007). Voucher specimens from this population of *M. vatia* have been deposited in the American Museum of Natural History, New York.

Spiders were released in a dense patch of wild marjoram *Origanum vulgare* of 2.1 m^2 area and 400 flowering stems located in the middle of this field. Their stems varied between 0.4 and 0.6 m in height and bore several small, terminal pinkish-purple (= light mauve: Smithe 1975) flowers in rounded panicles. These flowers bloomed profusely for several weeks from mid-July to early September. The patch attracted large numbers of potential prey for the spiders: bumblebees, butterflies of several species, sarcophagid and tachinid flies, and much smaller numbers of several other insect groups. During the study, only goldenrods *Solidago canadensis* flowered within several meters of the study area, none closer than one meter. Vegetation within a 1-m arc about the marjoram consisted of various grasses and low pasture rose bushes *Rosa carolina* that had completed flowering before the marjoram began to bloom. Thus, the site offered no nearby attractions to lure the spiders away from it. Adult female *Misumena* locate hunting sites primarily by the concentration of large insects at flowers (Morse 1988b).

Subjects and experimental setup.—I measured the adult carapace width of each individual used in this study and numbered its abdomen with a black Sharpie extra fine-point pen, a procedure that does not adversely affect them (Morse & Fritz 1982). Gravid adult female spiders used in this study had been placed on common milkweed *Asclepias syriaca* plants, enclosed by a 35 × 20 cm bag of white nylon tricot, shortly before building their nest on a leaf (Morse 1985) and laying their brood of eggs. I recorded laying dates and allowed the females to guard their nests on the milkweed leaves *Asclepias syriaca* for 1–26 days, the average time to emergence of *Misumena* young from their natal nests (Morse 1987). I measured and weighed these individuals immediately prior to egg-laying and weighed them again immediately after laying and before release into the patch of marjoram. I made these measurements in the laboratory, adjacent to the study area, and returned the spiders to the field immediately after weighing.

After weighing I released 20 of these post-reproductive individuals onto inflorescences in the marjoram patch in 2001 and 2004–2007, separating them from each other as much as possible. I only released 20 individuals per year because of the limited size of the test area and the number of individuals available, the latter a consequence of several other studies carried out simultaneously. Upon their release I marked each spider's position in the patch with a small flag, which allowed me to calculate the minimum distance it traveled (distance between previous and present spot) if it changed its location. I measured distances traveled because of the possibility that they would reflect differences in quality of hunting sites and hence gains in mass.

I monitored the released individuals in the patch of marjoram from 2–23 August, carefully searching the patch for the spiders every third day, weighing each individual found, measuring the minimal distance it could have traveled over that time, and replacing it in its current location, at the same time repositioning its flag to the new site if the spider had changed its location. On other days, I recorded the locations of any individuals observed, also searching the nearest goldenrod inflorescences for spiders that might have left the patch.

Sample sizes of several variables used in the analyses tallied to less than the 100 individuals released, because I did not record all of the variables from all of the individuals tested each year. Numbers ranged from 52 to 100.

I censused numbers of potential insect prey in the marjoram patch at approximately noon on every other day. The exact time of these counts varied between 11:30 and 13:00 h and depended on other projects carried on simultaneously. Prey recorded in these censuses weighed ~ 25 mg or more (bumblebees, butterflies, large sarcophagid and syrphid flies), since earlier work demonstrated that adult female *Misumena* cannot maintain their body mass on prey much smaller than these insects (Morse 1979) and that they do not choose among prey in the > 25 mg range. During 2002 and 2003, years in which I did not add post-reproductive *Misumena* to the site, I nevertheless counted the insects in the same way as in the years of spider additions.

Analyses.—I compared the among-year differences of A) percent daily loss in mass while nest-guarding (arcsin transformed) and B) percent daily gain in mass subsequent to release (arcsin transformed) with one-way ANOVAs, using proportional values to accommodate for the differences in size of the spiders. In the absence of significant among-year differences, I pooled the results from the different years in subsequent analyses. I then subjected the pooled samples to backward stepwise multiple regression analysis (Sokal & Rohlf 1995). I incorporated independent variables likely to account for differences in percent daily loss in mass during nest guarding and percent daily gain in mass after release. Initially these variables were 1) maximum mass before egg-laying, 2) mass after egg-laying, 3) mass at release into marjoram, 4) carapace width, and 5) days after laying (a measure of starvation period). After screening for collinearity ($r > 0.8$), I removed Independent Variable 2, mass after egg-laying, because of its strong correlation with Independent Variable 1, maximum mass before egg-laying.

Table 1.—Important variables of adult female crab spiders *Misumena vatia* used in this study.

Variable	*n*	Mean ± SE	Range
Maximum mass before laying (mg)	99	221.4 ± 5.99	114.8–365.7
Mass immediately after laying (mg)	81	74.8 ± 2.08	42.0–125.8
Mass at release into foraging site (mg)	100	68.6 ± 1.73	39.5–110.0
Time guarding after laying (days)	99	13.6 ± 0.68	1–26
Carapace width (mm)	100	3.4 ± 0.03	2.8–4.0
Distance moved (cm)	52	89.0 ± 8.42	9–244

Following a one-way ANOVA to test for between-year differences, I compared percent daily gain in mass with movement about the marjoram patch with a two-tailed paired *t*-test. Amount of movement might reflect an inability to find high-quality hunting sites (Morse & Fritz 1982). Since I could not find several individuals subsequent to their release in the marjoram patch, I tested for possible differences in numbers of missing individuals among years, using a *G*-test of independence. I then compared the two groups (recorded, not recorded) for possible differences in the set of independent variables noted immediately above, as well as percent daily loss of mass after egg-laying, using *t*-tests for the difference between two means. I looked for differences in large prey abundance among years using a *G*-test for goodness of fit, followed by a search for possible among-year differences in numbers of spiders recorded and prey numbers in the marjoram patch, using a *t*-test for paired comparisons. Such an outcome could result from differences in numbers of large insect prey. Means are reported ± SE.

RESULTS

Loss in mass during guarding stage.—I found no among-year differences in percent daily loss in mass during the nest-guarding stage (one-way ANOVA: $F = 1.98$; $df = 4, 72$; $P > 0.1$); thus, I pooled years in analyses of loss in mass. Of the several variables potentially related to percent daily loss in mass over the pre-release period (Table 1), time since laying and maximum pre-laying mass differed significantly in a stepwise multiple regression analysis (Table 2). The significant negative relationship between time since laying and rate of loss in mass resulted from the rate of loss decreasing over time (Fig. 1), and the weaker positive relationship (Fig. 2) resulted from larger individuals losing mass at a proportionately greater rate than the smaller ones. Other measures directly related to mass (mass at release into marjoram, carapace width) did not differ significantly (Table 2). The 19 individuals retained more than 20 days after egg-laying lost 17.3 ± 1.53% of their body mass, with a maximum of 28.4%.

Table 2.—Parameter estimates from a multiple regression model by standard least squares of percent daily loss in mass (arcsin transformed) of adult female *Misumena vatia* in relation to several variables. Model summary: $n = 77$, $R^2 = 0.18$, $F = 3.81$, $P < 0.01$.

Variable	Partial regression coefficient	Standard error	*t*	*P*
Intercept	2.497	0.921	2.71	< 0.01
Maximum mass before egg-laying	0.003	0.002	2.13	< 0.05
Mass at releasc	− 0.005	0.006	− 0.85	> 0.3
Carapace width	− 0.500	0.375	− 1.33	> 0.1
Days aftcr laying	− 0.028	0.009	−3.03	< 0.0

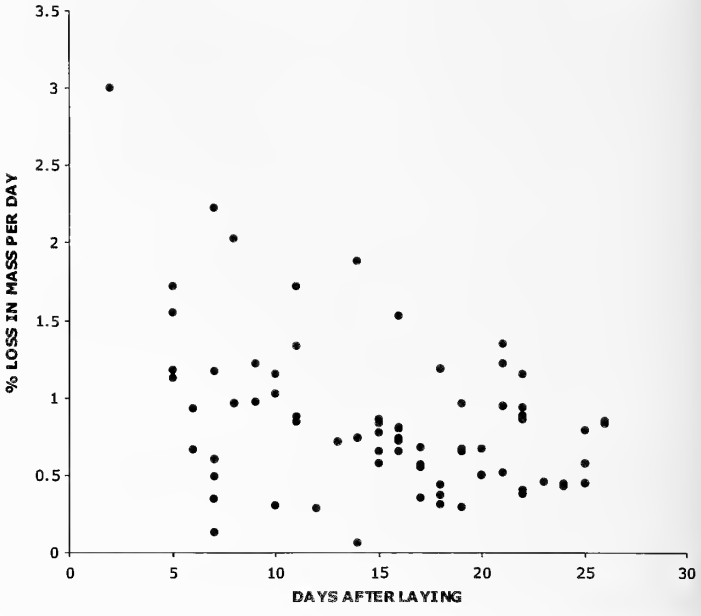

Figure 1.—Percent daily loss in mass of female crab spiders after laying brood of eggs. Mass measured immediately after eggs laid and at time of removal from nest for deployment to marjoram.

Gain in mass after release.—Testing the same variables as in the preceding section in the same way, I found no among-year differences in percent daily gain in mass subsequent to release of the post-reproductive spiders into the marjoram patch (one-way ANOVA: $F = 2.27$; $df = 4, 59$; $P > 0.05$). None of these variables exhibited a significant relationship with percent daily gain in mass subsequent to release in a stepwise multiple regression analysis (Table 3). Perhaps surprisingly, given the effect of time since laying on loss in mass, this variable did not significantly differ from gain in mass after release (Table 3).

Movement of individuals recorded after release.—I found no between-year differences in minimum distances moved in the patch of marjoram after release during the 2004–2007 seasons

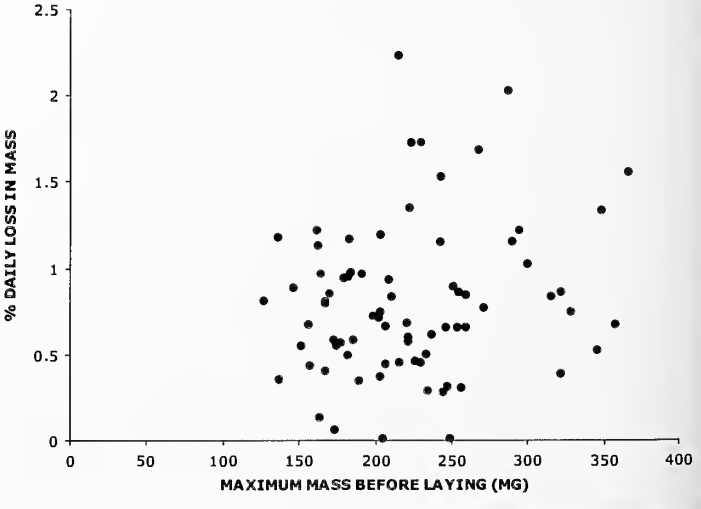

Figure 2.—Percent daily loss in mass of female crab spiders in relation to maximum pre-laying mass.

Table 3.—Parameter estimates from a multiple regression model by standard least squares of percent daily loss in mass (arcsin transformed) of adult female *Misumena vatia* in relation to several variables. Model summary: $N = 64$, $R^2 = 0.08$, $F = 1.20$, $P > 0.3$.

Variable	Partial regression coefficient	Standard error	t	P
Intercept	− 1.185	5.864	− 0.20	> 0.8
Maximum mass before egg-laying	0.013	0.011	1.19	> 0.2
Mass at release	− 0.030	0.037	− 0.81	> 0.4
Carapace width	1.491	2.370	0.63	> 0.5
Days after laying	0.013	0.058	0.22	> 0.8

(one-way ANOVA: $F = 0.25$; $df = 3, 47$; $P > 0.8$). (I did not record this variable in 2001.) The spiders varied greatly in the minimal distances traveled within the marjoram patch (9–244 cm); however, distance moved bore no relationship to percent gain in mass per day ($t = -0.19$, $df = 51$, $P > 0.8$ in a two-tailed paired t-test).

Individuals recorded after release.—I failed to find several spiders subsequent to their release (20 released each year), though the numbers of individuals seen after release varied among years (12, 9, 10, 16, 17: $G = 11.59$, $df = 4$, $P < 0.05$ in G-test of independence). Almost all the observed individuals occupied hunting positions among the flowers, notwithstanding the considerable effort expended in search. Since I often found temporarily missing individuals in subsequent searches, they apparently spent considerable periods in the dense, lower parts of the vegetation, away from the terminal flowers that attracted potential insect prey. I missed some individuals for two or three surveys in a row, only for them to appear on a later date. Although this uncertainty makes it difficult to calculate emigration rates from the marjoram patch, systematic searches of the nearby vegetation yielded only a single individual, found on goldenrod, over the five years. I returned that individual to its previous position in the marjoram patch, but subsequently found it away from the patch in goldenrod a second time.

No significant difference occurred between individuals recorded and not recorded after release in any of the variables measured (Table 4). They did not even differ in days since laying, a measure of post-reproductive age (those found = 13.4 ± 0.86 days, $n = 64$; those not found = 14.0 ± 1.16 days, $n = 36$).

Influence of large insect visitors.—Data on visits by large insect prey exist for the five years in which I monitored the spiders, plus 2002 and 2003 (Fig. 3). Numbers of insects differed widely among years ($G = 479.98$, $df = 6$, $P < 0.001$ in a G-test for goodness of fit. However, no relationship emerged between numbers of large insects visiting the flowers (bumblebees, butterflies, large flies) and the number of spiders seen once or more after their release ($t = -0.66$, $P > 0.5$ in a two-tailed t-test for paired comparisons). Percent daily gain in mass of these spiders varied only between 5.1 and 6.1, except for 3.7 in 2007, while numbers of large insects differed nearly six-fold over the census period. The higher proportion of spiders subsequently recorded in 2006 and 2007 (16 and 17 of 20) occurred during years of relatively low insect visitation, but those individuals were recorded in the marjoram for a length of time that did not differ markedly from the earlier years (mean = 10.0 days; range of 8.3–12.6 days over the total years of the study).

Table 4.—Characteristics of individuals recorded after release in marjoram patch and those not recorded after release. Sixty-four of the one hundred individuals were subsequently recorded. Two-tailed t-tests.

Factor	Number	t	P
Maximum body mass	98	−1.391	> 0.1
Body mass after egg-laying	80	−0.453	> 0.6
Body mass at release	99	−1.198	> 0.2
Days since laying	100	+0.445	> 0.6
Carapace width	99	−0.377	> 0.7
% loss/day after egg-laying	76	−0.682	> 0.4

DISCUSSION

Changes in mass.—Only the number of days since a spider had laid its brood, a likely correlate of how recently it had fed, and mass immediately before egg-laying significantly affected percent daily loss in mass subsequent to egg-laying. Although individuals naturally continued to lose mass, the rate of loss decreased over time, probably reflecting a decrease in metabolic rate. Anderson (1974) demonstrated that the metabolic rate of both *Hogna lenta* (Hentz 1844) and *Kukulcania hibernalis* (Hentz 1842) declined within a few days under starvation conditions in the laboratory, and it is reasonable to propose a similar pattern for *Misumena* as well. The greater rate of loss in mass of the larger individuals should reduce advantages they might gain over smaller individuals, either for survival or for conversion into offspring in a possible second brood. However, large individuals presumably have more resources to use in such a situation than small ones. As a

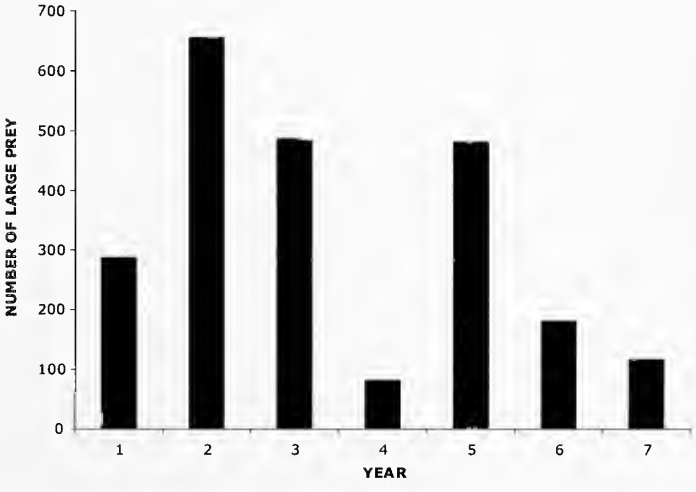

Figure 3.—Cumulative numbers of large prey (bumblebees, butterflies, large flies) at marjoram patch in noontime censuses over period of study in years 2001–2007 (##1–7).

consequence of their change in rate of loss in mass, my post-reproductive individuals probably did not lose enough mass to endanger their survival over the maximum time tested, 26 days, a period that matched the mean time between egg-laying and emergence of spiderlings from their nest sac (Morse 1987). The percent loss in mass of the individuals retained the longest (20 days or more) fell well below the 35–40% lost by post-reproductive female *Misumena* before succumbing (Morse 1987).

None of the variables tested significantly affected percent daily gain in mass among the released individuals. This lack of relationship to any of the variables contrasts strikingly with pre-oviposition gain in mass, for which strong correlations existed between gain in mass and key independent variables (Morse & Fritz 1982; Fritz & Morse 1985). The failure of the spiders to respond to the wide fluctuation in numbers of prey suggests that enough insects always visited the flowers that their abundance did not become an important factor in gaining mass for the spiders. The fluctuation in prey numbers was most likely ultimately driven by outbreaks of goldenrod beetles *Trirhabda* spp., which defoliated much of the surrounding goldenrod (Morse 2007), thereby reducing the major resources of the pollinators in the field and, hence, the food supply of the spiders.

Individuals recorded and not recorded after release.—Earlier studies on post-reproductive female *Misumena* retained in the same way as in this study (Morse 1994) revealed that of the individuals abandoning their nests over a 26-day period (45% of the total), half had died, and half had moved to other parts of the bags (they presumably would have dispersed if given the opportunity). That result suggests that several of the missing individuals died in the marjoram patch during the observation period, although I found no dead ones. Further, the missing individuals did not differ significantly in traits measured prior to release from those subsequently observed.

The general failure to find released spiders outside the marjoram patch, even on the nearest flowers, suggests that they seldom left the release site, a behavior similar to that of prereproductive adult females at rich hunting sites (Morse & Fritz 1982). Although anecdotal, the recovery of a single individual outside the patch, followed by a repeat recovery of that same individual outside the patch shortly after I returned it to its previous site in the patch, further suggests that I seldom failed to find individuals that had quit the site. Even though a high density of conspecifics in the patch might engender dispersal, prereproductive adult female *Misumena* not infrequently reach similar densities at sites with extremely high rates of prey visitation (Morse 2007).

Relationship to semelparity.—This data set is notable for the dearth of significant correlations observed, especially in post-reproductive gain in mass, consistent with the predictions of Fisher (1930), Williams (1957), and subsequent workers. The few significant relationships involved loss in mass prior to release and resembled the success enjoyed by individuals during the prereproductive part of the life cycle, a likely consequence of advantages accruing to individuals at that stage (Morse & Stephens 1996). These post-reproductive performances likely do little or nothing to enhance selection for producing a second brood.

Post-reproductive *Misumena* thus perform very much like semelparous forms, exhibiting few characteristics that would attain high fitness values if employed earlier in life. In themselves these properties should favor the evolution of semelparity, with progressively higher allocation to egg production. However, parental nest defense has high survivorship value for the young in these *Misumena* populations (Morse 1988a), which should counter selection to yet higher reproductive effort (% body mass devoted to brood) (Tallamy & Brown 1999). These spiders already exhibit an extremely high reproductive effort, in itself a trait exhibited by semelparous individuals (Roff 2002; Stearns 2002), relative to that of co-occurring species with comparable nesting strategies (Morse 2007). The extremely low resting metabolic rate of spiders (Anderson 1970) may facilitate nest guarding under conditions that favor semelparity. It may also facilitate their ability to lay a second brood as large as the first under experimental conditions (Morse 1994), although if individuals in the wild were constrained to lay large second broods, this trait should make iteroparity an even greater obstacle. Thus, characteristics that facilitate more than a random opportunity to become functionally iteroparous appear to be lacking in this population of *Misumena*.

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Unusual organization of scent glands in *Trogulus tricarinatus* (Opiliones, Trogulidae): evidence for a non-defensive role

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Abstract. The morphology of the scent glands of *Trogulus tricarinatus* (Linnaeus 1767) (Trogulidae), a small, soil-dwelling opilionid species, was investigated by means of serial histological semi thin-sections. The glands constitute paired prosomal glandular sacs that open to the body surface via one pore (ozopore) on either side of the body, dorsally adjacent to coxae I. Consistent with the generally recognized organization of scent glands in Opiliones, an anterior non-secretory region of the reservoir could be distinguished from a posterior secretory area, the latter characterized by a thick vacuolated epithelium. However, there are several unusual scent gland features in *T. tricarinatus*. First, the ozopores are hidden, with each being surrounded by a kind of external secretion atrium formed by a dorso-lateral integumental fold (dorsal limitation), coxa I (ventral limitation), and a wall of projecting cuticular papillae (outer lateral limitation). A horizontal slit ("secondary opening") between the top of this wall and the dorsal integumental fold is externally visible. Secondly, no fluid, but solid spherical structures that may represent condensed secretion are found in the reservoirs. Thus, the secretion must pass through the external atrium before reaching the outside, perhaps as a gas produced by slow sublimation of solid secretion boli. Scent gland organization in *T. tricarinatus*, especially the findings of an external atrium around the ozopores, is not consistent with use in chemical defence, as is generally assumed for scent glands of Opiliones, but indicates a possibly non-defensive role.

Keywords: Exocrine glands, chemical defense, opilionids, Palpatores, Dyspnoi

Large prosomal exocrine scent glands, also called defensive or repugnatorial glands, are an important synapomorphic character of Opiliones (Martens 1978). Although large and conspicuous, scent glands have been examined in only a few detailed histological studies. Clawson (1988) described the scent glands of two sclerosomatid species, and the scent glands of a few ischyropsalidid species were investigated by Lopez et al. (1980) and Juberthie et al. (1991). Recently, an ultrastructural study on exocrine glands of *Cyphophthalmus duricorius* (Cyphophthalmi) was published (Gutjahr et al. 2006).

In general, opilionid scent glands are considered a means for defense (e.g., Martens 1978). This view is based on 1) the characteristic morphological organization of glands that clearly show an "allomonal-type" gland construction, comprising undivided, intima-lined, large-scale reservoirs along with a central orifice and 2) emission of secretions that, in most cases, is inducible by mechanical disturbance and frequently is followed by distinct behavioral steps such as "leg dabbing" (sensu Juberthie 1961). In many Laniatores, cuticular grooves lead backwards from scent gland orifices and serve to divert the secretion on the body surface, leading to the generation of a protective chemical shield around the body (summary in Gnaspini & Hara 2007). Finally, and possibly most importantly, 3) the repellent properties of secretions against potential opilionid predators have been proven in bioassays and by behavioral observations, at least for some model species (e.g., Eisner et al. 2004; Willemart & Pellegatti-Franco 2006).

While these scent-gland properties seem to be consistent in Cyphophthalmi and Laniatores, the scent gland features of a large part of Palpatores, namely in some phalangiids and in the Dyspnoi, are quite cryptic. Glands and glandular openings (ozopores) may be inconspicuous and some species are apparently reluctant to discharge secretion, even in cases of heavy mechanical treatment (e.g., Kaestner 1931–1941). Especially in representatives of Dyspnoi, such as in Trogulidae, a discharge of secretion has never been observed (Pabst 1953).

Recent studies have shown that the functional repertoire of opilionid scent glands may exceed pure chemical defense. Such additional functions may include the production of antibiotics (e.g., Estable et al. 1955; Fieser & Ardao 1956), alarm pheromones (Machado et al. 2002), aggregation and sex pheromones or pheromones for territorial marking (Bishop 1950; Holmberg 1986; Juberthie et al. 1991). Exocrine glands of arthropods producing the latter types of pheromones, however, typically exhibit a glandular organization distinctly different from opilionid "allomonal"-type scent glands (e.g., Percy-Cunningham & MacDonald 1987). Thus, especially with respect to the scent glands of certain Dyspnoi (such as non-scenting Trogulidae), a possible change of glandular function and role may not only be indicated by a reluctance to discharge secretion, but also by a distinctly different morphological organization of glands.

In the present study, we investigated the scent glands in a model, non-secretion discharging species, *Trogulus tricarinatus* (Linnaeus 1767) (Opiliones, Trogulidae), and we here report on its aberrant scent gland construction.

METHODS

Specimens of *Trogulus tricarinatus*, including adults of both sexes and juveniles, were collected from soil samples from different locations in Carinthia and Styria, Austria, by hand or

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using a Berlese apparatus. Specimens were fixed in Bouin's solution for 24 hours, washed, dehydrated, and embedded in LR-white soft grade (London Resin Company Ltd., Berkshire, England via Gröpl, Tulln, Austria). Blocks were sectioned using glass knives and a rotary microtome (Leica Jung 2065 Supercut, Leica, Vienna, Austria), leading to serial cross and longitudinal sections of 2.5 µm thickness. Sections were stained with toluidin blue (Lactan, Graz, Austria). Scent glands and surrounding structures were reconstructed from sections according to Honomichl et al. (1982) and by 3D-reconstruction software (Amira 4.1). For scanning electron microscopy (SEM), fixed, washed, dehydrated and air-dried specimens were mounted on aluminium stubs, sputtercoated (AGAR sputtercoater, Gröpl, Tulln, Austria), and examined with a Philips XL30 ESEM (Philips/FEI, Vienna, Austria) at high vacuum mode and 20 kV accelerating voltage.

RESULTS

Topography and size of glands.—One prosomal sac-like scent gland is situated directly beneath the integument on each side of the carapace. Each extends backwards 500–700 µm from the level of the first legs, which corresponds to 10 to 15% of the body length (Fig. 1). The glandular sacs (g) are rather narrow in their most anterior region (diameter about 50 µm), but reach a maximum width of more than 200 µm in more posterior parts. Only minor sex-related differences were noted and are limited to differences in shape due to spatial demands of the closely adjacent genital systems. In general, the sacs are moderately sinuate and laterally flattened (Figs. 1, 6, 7).

Glandular openings (ozopores) and "secretion atrium".—Ozopores (o) are oval-shaped with a maximum diameter of about 50 µm and are located nearly dorsal to the coxae of leg I (cx I). In adults, these openings are not visible externally but are hidden in a kind of secretion atrium (a). Specifically, this atrium (see Fig. 2) is built of 1) the dorso-lateral integumental folds (f) of the anterior carapace (= dorsal limitation), 2) coxa I (= ventral limitation), and 3) a heavy wall of cuticular papillae (= c and cp: outer lateral limitation). These papillae cover large parts of the cuticle and represent elongated, hollow, column-like structures, each 50–70 µm in height and about 30 µm in diameter ("Druesenwaerzchen" sensu Schwangart 1907). The cuticular papillae comprise the outer lateral wall of the atrium, eaeh papilla bordering the next without a gap and projecting upwards from coxae I (Figs. 2, 9, 10). Only a narrow, sickle-shaped slit (so) of 5–40 µm width and 65–200 µm length between the dorsal integumental fold and the top of the wall of cuticular papillae remains open and ean also be seen from the outside (Figs. 2, 8–11). This slit represents the external opening of the atrium, and thus, a kind of "secondary" opening of the scent glands. In addition, in the most anterior part of the atrium, its cavity is ventro-medially not completely closed but is connected to the camerostome through a groove. In general, the cavity of the atrium is spherical to egg-shaped, with a horizontal extension of about 140–190 µm; width and height of the cavity are about 40 and 200 µm, respectively. The inner surface of the atrium is covered with cuticular spines that mainly project from the ventral (coxa) and dorsal (integumental fold) walls. Scanning electron micrographs of the atrium and the secondary slit-like orifice, histological seetions and a 3-D reconstruction of the atrium and

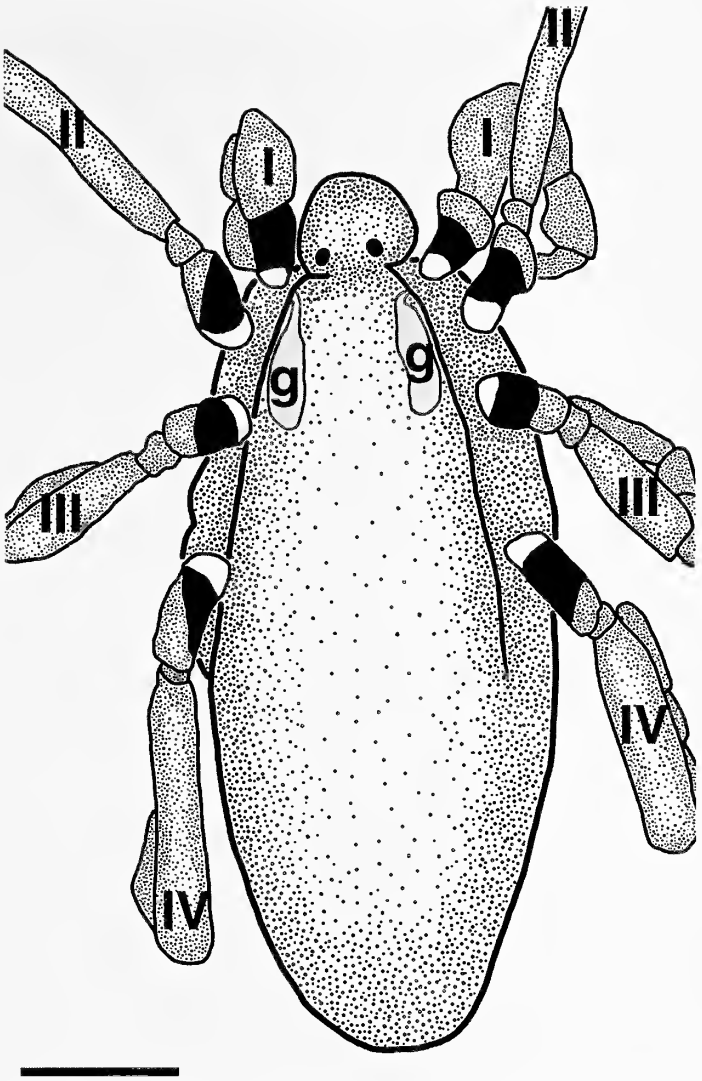
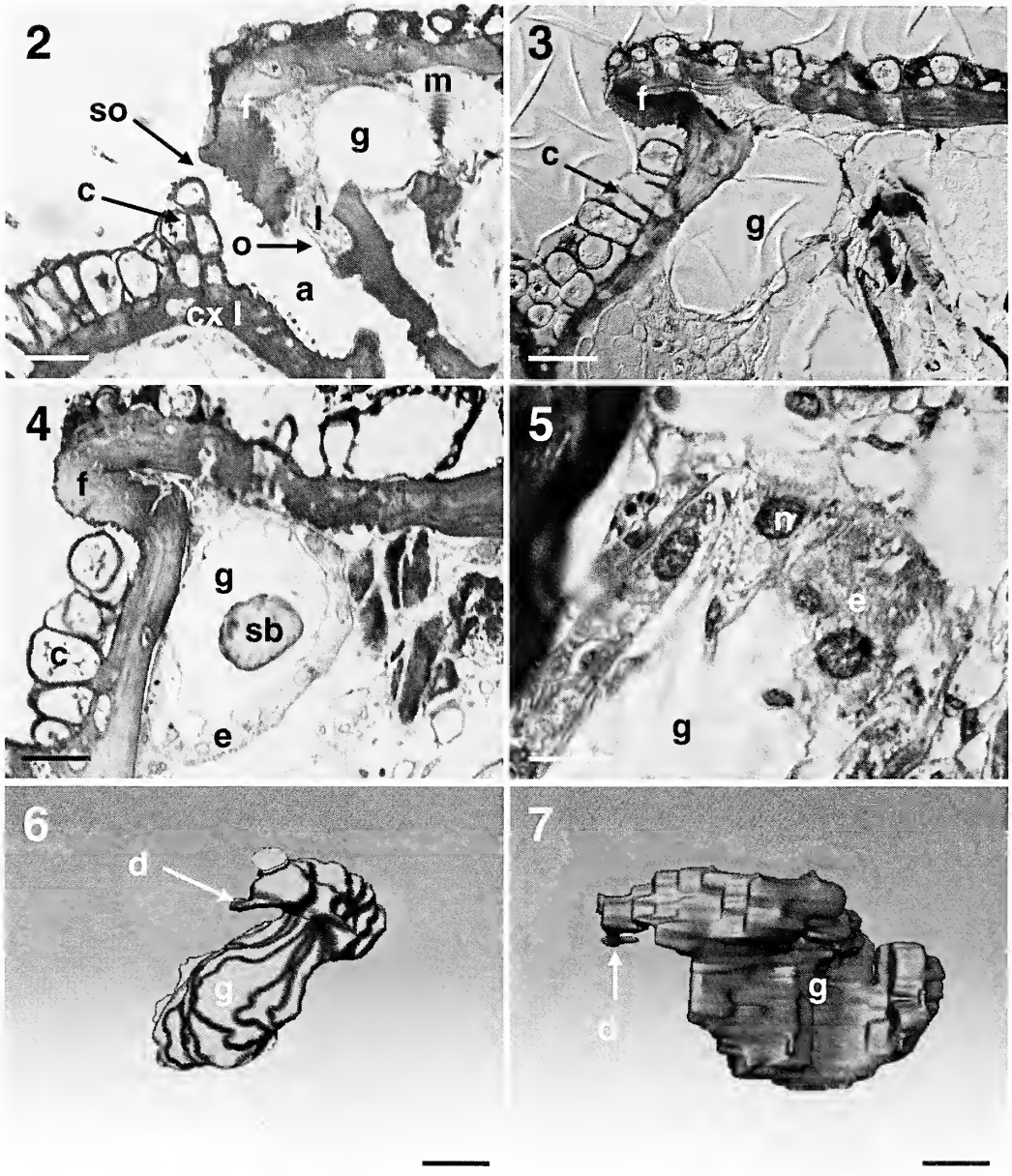


Figure 1.—Position, size, and shape of prosomal scent gland in *Trogulus tricarinatus* (semi-schematic). Male, dorsal view. Position of sac-like scent glands (g) is indicated. Abbreviations: I–IV = legs I–IV, g = scent gland. Scale bars = 1 mm.

adjacent structures are given in Figs. 2, 8–11. In juveniles, cuticular papillae (and thus, also the atrium itself) are lacking.

Reservoir: excretory duct, non-secretory and secretory areas.—Each scent gland mainly comprises a large intima-lined sac (g, reservoir) surrounded by non-secretory epithelium anteriorly and secretory epithelium posteriorly. The most anterior part also includes a short, narrow excretory duct (d) that latero-ventrally branches off the reservoir to reach the ozopores (Figs. 2, 6, 7). Muscles (m) attach at the inner side of the dorsal integument and extend transversely to the region of the duct (Fig. 2). They are only present in the most anterior region of glands, (i.e., in the narrow zone near the excretory duct and the pore orifice). A kind of "lid" (l, not further specified, multi-cellular tissue) seals the gland opening; the muscles, however, do not attach on the lid, but ventrally adjacent to it on the cuticle.

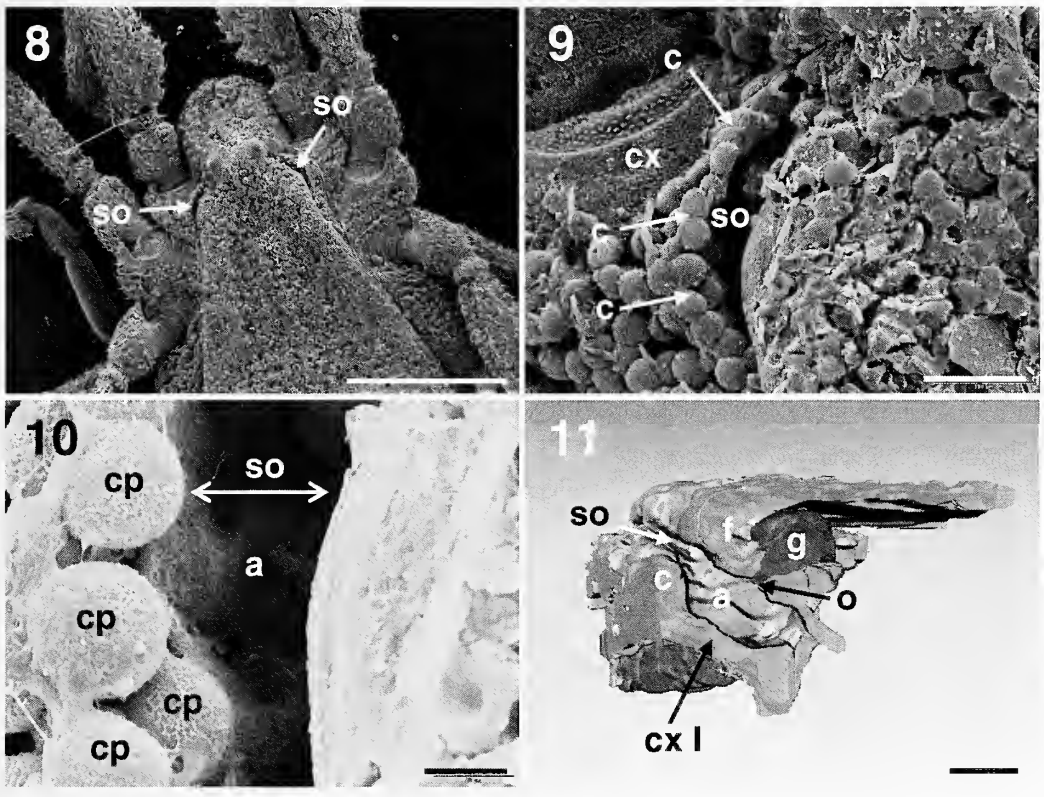
The non-secretory area of the glands (Fig. 3) either shows an intima layer only (= no epithelium visible) or, a bit more posterior, a single-layered epithelium (e). In the middle part of



Figures 2–7.—Histological sections and reconstruction of scent glands in *Trogulus tricarinatus*. 2. Cross section through left scent gland (g) in its most anterior part at the height of coxae I (cx I); pore orifice (= ozopore, sealed by a lid) leads into the secretion atrium (a). In this region, the atrium is ventrally not completely closed (connecting to the camerostome); laterally it is bounded by a wall of cuticular papillae (c). Note the slit-like secondary opening (so). 3. Cross section through the anterior region of left scent gland, showing the non-secretory area. 4. Cross section, left scent gland in a more posterior region, showing the secretory area. Thick glandular epithelium (e) and secretion bolus (sb) visible. 5. Detail of secretory epithelium with grained and vacuolated epithelial cells (e) and large nuclei (n). 6, 7. 3D-Reconstruction of right scent gland from histological sections, surrounding structures omitted: 6. Frontal view; 7. Lateral view from the inner side. Abbreviations: a = secretion atrium, c = wall of cuticular papillae, cx I = coxa I, d = excretory duct, e = epithelium of scent gland reservoir, f = integumental dorsal fold of the carapace, g = scent gland reservoir, l = lid, m = muscles, n = nucleus of epithelial cell, o = scent gland orifice, sb = secretion bolus, so = secondary opening. Scale bars: 100 μm (6, 7), 50 μm (2–4), 10 μm (5).

the glands, the epithelial cells are small and flat, reaching a height of up to 10 μm and a width of 20–30 μm. These epithelial cells do not show apparent granulation or vacuoles when observed under the light microscope. The thickness and development of the epithelium as well as the folds of the intima distinctly increase from the middle part of glands to their posterior end. The posterior part obviously represents the secretory area of the glands (Fig. 4), as indicated by conspicuously large epithelial cells that are cuboidal (maximum height and width 60 μm) and show distinct plasmatic structures (large granules and vesicles) and large nuclei (*n* in Fig. 5). In this region, the intima protrudes in multiple folds into the reservoir lumen.

While the reservoirs appear to be largely empty (but not collapsed) in histological sections (at least, these do not contain stainable liquid secretion), a few (1–4) compact, slightly stainable spheres (sb) of about 50–70 μm in diameter could be found in the posterior part of the reservoirs (Fig. 4).



Figures 8–11.—Secretion atrium and secondary orifice in *Trogulus tricarinatus*. 8. SEM of the prosoma of a male individual, dorsal view. Arrows mark the secondary, slit-like orifice of the secretion atrium. 9. SEM, detail of left secondary orifice of secretion atrium. Note the outer, lateral wall of adjacent cuticular papillae that project from coxa I. 10. SEM, one fresh look into the secondary orifice. 11. 3D-Reconstruction of the right scent gland and surrounding integumental structures, including the secretion atrium (a) with secondary opening (so), antero-lateral view (reconstruction from serial cross sections). Opening of gland (ozopore, o) into the external secretion atrium (a) is visible. Abbreviations: a = secretion atrium, c = wall of cuticular papillae, cp = singular cuticular papilla, cx I = coxa I.f = integumental dorsal fold of the carapace, g = scent gland reservoir, o = scent gland orifice, so = secondary opening, Scale bars: 1000 μm (8), 100 μm (9, 11), 20 μm (10).

DISCUSSION

Internal organization of scent glands in *Trogulus tricarinatus*.—The internal organization of scent glands in *T. tricarinatus*, mainly comprising glandular sacs with central orifices, corresponds to anatomical data known from other Opiliones (e.g., Juberthie 1961, 1976; Clawson 1988; Gutjahr et al. 2006). Such general scent gland features obviously include large glandular reservoirs that are divided into a non-secretory and a secretory area and characterized by differentially developed glandular epithelium. The anterior area of the reservoirs in *T. tricarinatus*, showing intima or flat epithelial cells only, apparently corresponds to the non-secretory area of opilionid scent glands as, for instance, described in *Cyphophthalmus duricorius* Joseph 1868 (Cyphophthalmi) and in *Leiobunum* spp. (Phalangioidea: Sclerosomatidae) (Clawson 1988; Gutjahr et al. 2006). The flat cells may be classified as euticle-supporting cells that are responsible for sustaining the thin intima that eovers the lumen of the reservoirs. Furthermore, the available literature indicates that the secretory area of the scent glands (generally located in the posterior part of glands) consists of both small cuticle-supporting cells and large-grained secretory cells, with the latter cell type also being characteristic of the posterior area of glands in *T. tricarinatus*. Secretory cells in glands of *C. duricorius*, for instance, are reported to contain many mitochondria, lipid droplets, and granules, either being electron-lucent or electron-dense (Gutjahr et al. 2006); for *T. tricarinatus*, comparably structured secretory cells are expected but this remains to be studied by ultrastructural methods.

Gland construction vs. biological role in *Trogulus tricarinatus*?—As outlined above, opilionid scent glands are generally considered to show a morphological organization that is typical of defensive glands found in arthropods. By contrast, the scent glands of *T. tricarinatus* (and possibly other Trogulidae) exhibit a few peculiarities: ozopores are covered by a secretion atrium, a cavity between the cuticle and the cuticular papillae that cover the cuticle. Thus, in case of secretion discharge (if occurring at all), the secretion would have to pass through the atrium before reaching the body surface. Due to these morphological peculiarities, the secretion can be neither easily nor rapidly expelled nor transferred to a potential predator. To our knowledge, such an atrium surrounding or covering the scent gland orifices has not been described elsewhere in Opiliones. In scanning electron micrographs, the slit-like external openings of the atrium are clearly visible; these obviously represent secondary openings for potentially discharged secretion. Such atria along with (secondary) openings can also be found in other adult Trogulidae (unpublished observations), whereas these are clearly absent in juveniles. In these terms, a scanning electron micrograph of the ozopore of *T. nepaeformis* in Eisenbeis & Wichard (1985) is most likely derived from a juvenile individual.

In distinct contrast with *T. tricarinatus*, ozopores tend to be visible and easily accessible from the outside in most other Opiliones, and are especially conspicuous in Cyphophthalmi (i.e., openings are located atop protruding tubercles, perfectly suited for defense). Also the modes of secretion delivery appear to be especially well adapted for defense in Cyphophthalmi and Laniatores, where secretions are either extruded more or less forcefully from ozopores as fine jets or as droplets or are transferred to the offender by leg dabbing (e.g., Juberthie 1961, 1976; Eisner et al. 1971, 1977; Acosta et al. 1993; Gnaspini & Cavalheiro 1998;). In contrast, *T. tricarinatus* does not emit secretions when mechanically treated or squeezed (Pabst 1953; original observations). These peculiarities strongly suggest a non-defensive role for the glands.

Secretion and secretion chemistry in *Trogulus tricarinatus*?— A further important argument against a defensive role of scent glands in *T. tricarinatus* concerns the presence and the (possibly solid) state of secretions. In general, defensive exocrine glands of arthropods produce and store liquid secretions, or at least, also contain solvents (diverse short-chain compounds) in which solid (or long-chain) compounds are dissolved. This situation is also realized in scent glands of the majority of Opiliones, even though rather viscous (but not solid) scent gland secretions have been reported from Laniatores. In Gonyleptidae, scent gland secretions are mixed up and diluted by enteric fluid before application (e.g., Eisner et al. 2004). Chemically, phenols and benzoquinones predominate within laniatorid secretions, while acyclic components and, at least in *Phalangium opilio* Linnaeus 1758, also naphthoquinones (Wiemer et al. 1978) are produced by phalangioids (for a summary see Gnaspini & Hara 2007). In Cyphophthalmi, both acyclic ketones and naphthoquinones are emitted (Raspotnig et al. 2005). No studies, however, on scent gland chemistry are available for Dyspnoi. This apparent lack of published information on Dyspnoi may be due, at least partly, to the production of a solid secretion, which leads to a "reluctance" or inability of the animals to discharge the secretion and to methodological difficulties in accessing them. So far, apart from *T. tricarinatus*, solid secretion boli in scent glands have also been found in some species of *Ischyropsalis* (Juberthie et al. 1991) but are expected to occur in further representatives of Dyspnoi, as well. For these solid secretion-producing Dyspnoi, a completely different, highly unusual system for emission of scent gland secretion may have evolved. Juberthie et al. (1991) speculated that solid secretion in scent glands may be released by slow sublimation and, thus, may be emitted as a gas. This mode of emission is currently classified as a distinct type, namely "the type which produces a scent without fluid production." Gnaspini & Hara (2007) considered this unusual mechanism of emission to be important for generating a chemical shield around the body, possibly protecting the emitter from predator attacks but also from microbes and fungi that are present in the subterranean environment.

In these terms, the slightly stainable spherical structures in the glandular reservoirs of *T. tricarinatus* may in fact represent a condensed (or crystalline) solid secretion, even though an artificial formation of these solid boli in the course of the histological preparation procedures (e.g., by precipitation or dehydration of secretion products) has to be considered as well. However, for the time being, the mechanisms of emission of presumably solid secretion (as described above) remain very speculative, the more than preliminary chemical investigation into scent glands of *T. tricarinatus* (based on hexane whole body-extracts) did not show any compounds accessible to gas chromatography (unpublished observation).

CONCLUSIONS

Taken together, the unusual gland construction (i.e., a secretion atrium covering the ozopores along with possibly solid secretion) and the observation that mechanical disturbance does not induce noticeable emission of secretion, strongly indicate a function other than chemical defence for scent glands of *T. tricarinatus*. More likely biological roles of scent glands in *T. tricarinatus* (and possibly also in other Trogulidae) may include territorial marking, as already proposed for subterranean ischyropsalidids (Juberthie et al. 1991), or even the production of aggregation pheromones (e.g., Bishop 1950; Holmberg 1986). Sexual communication, also often discussed (Pabst 1953), is probably not consistent with scent glands of *T. tricarinatus* as these glands do not show sexual dimorphism. In terms of an evolutionary interpretation of our findings, costly chemical defense may have become less important in the already well-defended trogulids (heavy sclerotization, soil incrustation, and cryptic lifestyle), and novel scent gland functions other than defense may have evolved.

ACKNOWLEDGMENTS

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The costs of moving for a diurnally cryptic araneid spider

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Abstract. In orb web spiders that recycle webs and thus minimize the material costs of web relocation, the characteristics of their temporal movement patterns between web sites ean be used to examine otherwise hidden costs. Previous studies have shown that one such cost is the extra risk from predation. An unusually long average residence time at web sites is one indicator of cost. In some cases the pattern of movements also appears to be indicative of high costs, similar to those experienced by spiders that do not recycle web proteins. Nocturnal *Poltys noblei* Smith 2006 (Araneidae) spiders are heavily reliant on good camouflage in their exposed daytime hiding positions. Thus the risk of moving to an unknown site where the spider may not match its background may impose a large cost on relocation. The temporal pattern and frequency of relocations of *P. noblei* in northern Sydney are compared to those reported for other orb web species. *Poltys noblei*, on average, is found to have a long residence period, and the pattern of movement of larger individuals in this species is found to be random. These data support the idea that moving is costly for this species. Finally, the seasonal timing of movements is examined for *P. noblei*. It is found that most spiders relocate in spring but it is unknown if this is to seek a better web site or for the spider to avoid predation.

Keywords: Web site tenacity, *Poltys*, seasonality, camouflage, material costs, predation

Spiders have often been used as model organisms when examining facets of predator-prey interactions and optimal foraging theory, both as predators (e.g., Olive 1982; Janetos 1982a) and as prey (e.g., Rypstra 1984; Wise & Chen 1999). Web building spiders have especially attracted the attention of researchers, in part because many are relatively easy to find and work with in the field and in the laboratory. Some rebuild all or part of their webs almost daily and so have the potential to react quickly to applied stimuli. A variety of models and ingenious measurement techniques have allowed researchers to estimate aspects of the cost of web construction with respect to the expenditure of silk and energy (e.g., Tanaka 1989; Nakata & Ushimaru 1999, 2004).

When a spider moves to a new web site there are potential costs from loss of hunting time, risks in entering an area of unknown quality with possible predators, as well as the costs in silk production and energy expenditure. For spiders that build materially expensive webs and do not recycle silk proteins, the high cost of silk and associated energy investment appears correlated to long web site residence times (Janetos 1982a; Tanaka 1989). In many orb web building species in the families Araneidae, Tetragnathidae, and Nephilidae ingestion of most of the web occurs before the spider moves away from a web site. The silk proteins, therefore, are largely recycled (Peakall 1971 in Janetos 1982a). This minimization of material costs has allowed researchers to focus on the other factors that affect orb web spiders' decisions to move, such as the effects of disturbance (e.g., Enders 1976) or prey abundance (McNett & Rypstra 1997). Two sources of information have most frequently been utilized: the temporal pattern of the movements and the frequency of relocation.

Temporal pattern of movements.—Janetos (1982a) showed that orb web building spiders with relatively low material costs of relocation may show non-random patterns of residence times at web sites, either tending to move on more quickly than expected, or staying much longer than expected. The implication of this finding is that these species are not constrained by costs and can move whenever it is most appropriate in terms of prey abundance or other factors. In contrast, some sheet-weaving spiders (Linyphiidae), which do not recycle their silk proteins, have a much greater energy cost when moving to a new site (Janetos 1982a). Accordingly, the relocation patterns of these sheet-weavers did not differ significantly from that expected due to random events (i.e., the cost of abandoned silk and energy is a strong deterrent to relocation unless necessitated by other factors). Based on this premise, a spider that recycles silk but has a random pattern of movement nonetheless may have a high cost of moving due to some other factor. An increased risk of predation during and after relocation was identified as this factor in the case of the orb web spider *Nephila clavipes* (Linnaeus 1767) (Vollrath & Houston 1986).

Frequency of relocation.—In work on orb web spiders, the frequency of relocation, or its inverse, the average length of residence at a site, has been used to demonstrate a response to factors such as changes in prey levels (Olive 1982; Vollrath 1985), web damage (Enders 1976), and intraspecific interactions (Smallwood 1993). These are among the many factors that together influence the suitability of a site for any particular spider at any given time (Riechert & Gillespie 1986). What may be most difficult to quantify are the negative influences, (i.e., those such as an increased risk of predation that could cause a spider to move less frequently than might otherwise be expected). These factors may be easiest to examine indirectly by comparing the habits of different species and their respective life histories, and considering the differences among them. As an example, Miyashita (2005) found that the likelihood of risk-taking in two *Nephila* Leach 1815 species appeared to correlate to their life histories—females of *N. pilipes* (Fabricius 1797) need to grow fast to reach the normally large adult body size, and this species is more likely to risk moving than the sympatric species *N. clavata* L. Koch 1878, which is smaller and may be able to afford periods of suboptimal growth.

Web site residency times are given as examples in Table 1. Most are for orb web spiders that recycle their silk; other web

Table 1.—Examples of "natural" (i.e., undisturbed) average lengths of web site residencies (days or nights) recorded for various orb web spider guilds or species (Ar = Araneidae, N = Nephilidae, Te = Tetragnathidae) and exemplars from the Agelenidae (Ag), Linyphiidae (L) and Theridiidae (Th). Entries based primarily on adult female spiders are in bold. Entries are ordered from shortest to longest mean residence time. Figures are calculated or extrapolated from a variety of formats given in the original cited studies. Explanatory notes: † Original figures are for web site tenacity (probability or percentage of spiders remaining per day, Enders 1973). Mean residence = 1 / 1 – prob. (wst). In Enders 1975, 1976 there are often two sets of figures, one set referring to individual spiders on certain nights, the second to gross pooled observations. Here only the latter kinds of figures are used, as these are generally in accord with the methodologies of other authors. # Mix of adults and juveniles. * Original figures are for mean days per residence. ^ Original figures are for turn-over (probability or percentage of spiders leaving per day). Mean residence = 1 / prob. (turn over). ** No calculation made in original paper: extrapolated from figures in text and based on few actual spider movements.

Species (Family) or guild	Mean length of residency (days or nights)	Reference	Notes
Orbweavers (Ar, Te, Uloboridae)	2.2 to 2.4*	Janetos 1982a	1978 and 1979; juvenile and sub- adult
Argiope aurantia Lucas 1833 (Ar)	2.6 to 4.5†	Enders 1975	June dates, 5th instar (from text)
***Argiope aurantia* (Ar)**	**3.4 to 7.7†**	**Enders 1976**	**control regimes (two field experiments)#**
***Tetragnatha elongata* (Te)**	**3.8***	**Smallwood 1993**	**low density of spiders, prey-poor habitat**
***Cyclosa argenteoalba* (Ar)**	**4.3^ to 5.6^**	**Nakata & Ushimaru 2004 & 1999, respectively**	**controls from separate field experiments**
Sheetweb weavers (L)	4.8 to 5.0*	Janetos 1982a	1978 and 1979; sub-adult and adult
Argiope aurantia (Ar)	5.3 to 14.3†	Enders 1975	August dates, probably subadult females, 8th to 9th instars
***Micrathena gracilis* (Walckenaer 1805) (Ar)**	**6.7* to 8***	**Hodge 1987b & a, respectively**	**control figures from each experiment; informal longest residency estimate of "weeks"**
***Argiope trifasciata* (Forskål 1775) (Ar)**	**8.7***	**McNett & Rypstra 1997**	**control replicates**
Nephila clavipes (N)	16*	Vollrath 1985	spiderlings in prey-poor habitat (enclosures)
Cyclosa octotuberculata (Ar)	16.9^	Nakata & Ushimaru 2004	juveniles (probably subadult)
Latrodectus revivensis (Th)	17.9*	Lubin et al. 1993	juveniles; probably affected by marking procedure
***Tetragnatha elongata* (Te)**	**17.9*^**	**Gillespie & Caraco 1987**	**low density of spiders, prey-poor habitat**
***Cyclosa octotuberculata* (Ar)**	**26.3^**	**Nakata & Ushimaru 2004**	
***Latrodectus revivensis* (Th)**	**44.1***	**Lubin et al. 1993**	**probably affected by marking procedure**
Nephila clavipes (N)	58.8**	Vollrath 1985	spiderlings in prey-rich habitat (enclosures). Longest recorded periods ≥ 42 days
***Agelena limbata* Thorell 1897 (Ag)**	**143 to infinity^**	**Tanaka 1989**	**adult spiders did not relocate**

builders are included for comparison. Even among the orb web builders a wide range of variation can be seen between those at the top of the table, which move most frequently, and those at the bottom with the longest residency times. In this paper, I examine the frequency and pattern of the web site movements of the araneid spider *Poltys noblei* Smith 2006 in bushland near Sydney, Australia. I compare the results with those of other species in Table 1 and discuss the risks of predation and the role of camouflage in prolonging web site residence times. Unlike many other spiders, *P. noblei* may over-winter at almost any size (Smith 2006b). The data gathered for the web site tenacity study is useful for examining the seasonality of movements of these spiders through the year.

METHODS

Spiders of the genus *Poltys* C.L. Koch 1842 are nocturnal orb web builders that remove their web around dawn and rebuild it each evening. *Poltys noblei* and other southern species inhabit bushland areas where trees and bushes commonly have patches of dead twigs. During the hours of daylight, when not in a web, the spiders rest camouflaged by shape and color on a bare, dead twig, often in an exposed position (Fig. 1a). *Poltys* males are small and can mature in just a few weeks if emerging during the summer months, but females have a longer lifespan, which in *P. noblei* probably lasts from one to two, or even more, years. Spiderlings are similar in abdominal morphology but a wide range of abdominal shapes and coloration develops as individuals grow towards maturity (Fig. 1 a–d; Smith 2006a, b). This intraspecific variation is likely to be important for the effective camouflage of spiders in the field.

Short-term observations of residence time.—Three periods of overnight transects were undertaken, an 8-night pilot study during autumn 2000, then 10-night periods in spring 2002 and autumn 2003. The sites were all located in the northern Sydney area, two in the Ku-ring-gai Chase National Park (Myall Track [33°40′18″S, 151°08′06″E], and Resolute Picnic Area on West Head [33°34′50″S, 151°17′05″E]) and one on the Waitara Creek Fire trail ([33°42′51″S, 151°05′23″E] the site detailed under "Long-term observations" below). Each transect route was surveyed several times through the night from dusk to daylight and the positions and activities of *Poltys* specimens were recorded on each pass. Web details and damage were also recorded as additional information. Following individuals at regular intervals from sunset to sunrise minimized the possibility that spiders were swapping sites without my knowledge since spiders are usually sedentary during the day. *Poltys noblei* is the only species in the genus recorded from this area (Smith 2006a). Specimens from these sites or close by, examined during the revision of Australian *Poltys* referenced above, are deposited in the Australian Museum.

Figure 1.—Female *Poltys noblei*. a, in a typical position on an exposed dead twig hanging over a track in the Ku-ring-gai Chase National Park near Sydney (right lateral view). b–d. typical specimens showing some of the variation in shape and color pattern, b and c show mainly dorsal abdomen (apex downwards), d is laterodorsal but with most of flank lost in shadow. Photo 1b by Ramon Mascord.

Long-term observations of residence time.—The long-term study was run along 400 m of the Waitara Creek fire trail, a remnant of urban bushland connected to the Berowra Valley Regional Park, between Hornsby and Normanhurst in the northern fringes of Sydney. This site was surveyed at approximately 7–10 day intervals from April 2002 to April 2004 (112 transects at an average of 8.49 day intervals) and then observations were continued on just a few selected spiders until the last had disappeared in late November 2004. Transects were started at least one hour after dark, later if possible to ensure that most specimens had already made webs, and generally on nights with suitable weather conditions for locating spiders. The details of each *Poltys* seen along the route were recorded. The temperature was noted at the beginning of each survey, at the turn-around point, and again on return to the start. Because of public access to the area and not wishing to draw the attention of potential bird predators to the locations of spiders, web locations were not marked and I avoided seeking out the specimens during the day (although a few were easily visible, which allowed further confirmation that the same specimen was using the site throughout the putative period of residence). Instead, web locations were described or sketched in relation to vegetation features. No attempt was made to mark specimens for a number of reasons (see below), but abdominal shape was noted. The approximate size of each specimen was estimated by eye, without the aid of templates; hence the size ranges used in the analysis are approximate. Slight changes in web site within the same bush or tree (up to about 20–30 cm for a small spider or 50–100 cm for a larger specimen) were noted but were not considered moves unless there were other reasons to suspect that the specimen in the new site was not the original, or that the specimen was now using a different resting position.

Although the long term transects were initiated after only the pilot study of the short term surveys was completed, the further 10-day short term studies confirmed that these

observations were valid. Overall, the short-term observations were found to indicate that (i) many spiders use the same, or a closely adjacent, web site night after night; and (ii) the likelihood of a similarly sized and shaped spider moving into a vacated web site soon after departure of the first was small unless there was a high local population density. Therefore, it was indicated that in general it was possible to monitor individual spiders without marking them, even though this introduced a small amount of uncertainty into the results. Marking spiders was decided to be unsuitable for this study because of the increased likelihood of relocation of disturbed specimens (and the likelihood of repeated disturbance when trying to get close enough with a bright light to confirm specimen identity), as well as potential disruption of camouflage and the likelihood of injury to small specimens.

Data analysis.—For the short-term transects, the average web site residence time for each transect site was calculated (in nights). Mean residence = total spider observation nights/total departures. For the long-term study, all calculations were performed using the average sample period as the unit of residence time (1 sample period = 8.49 nights). The sample mean and standard deviation were calculated for all spiders with unambiguous records. This excluded specimens for which the moving-in date was unknown (i.e., they were already present on the first transect night), or those for which there was likely to have been interference from conspecific spiders.

Two size classes were recognized, based on the field estimates. The "Small" class contained spiderlings, juvenile males (which cease making webs and become mobile when they mature), and juvenile females of a similar size. Therefore, small spiders in this context are those up to instar two or three (post emergence). This size-class cut-off point may be important as the abdomens of females are beginning to differentiate in shape at this size (Smith 2006b) and camouflage may begin to play a more important role. The "Large" class, therefore, comprised only juvenile and adult females. Some spiders grew from one class into the next while resident at a single web site. The class used here is the size at arrival.

The distribution of residence times of Small spiders was compared against those of the Large class using the χ^2 test on contingency tables and pooling most columns with expected values < 5 (note: it is not necessary to remove all expected values less than 5, Parker 1979). All subsequent tests used the two size classes separately.

For each size class the recorded pattern of residence times was compared with a random hypothesis, following the methods of Janetos (1982a) and Hodge (1987a, b). This method is based on the expectation that compounded random events such as web damage or disturbance by a predator should result in spider movement events that can be explained by a Poisson process (Janetos 1982a). A negative exponential series was generated (using the "expondist" function in Microsoft Excel), which models the expected distribution of spider movement events over time according to this random hypothesis. This distribution of class frequencies was then compared with that collated from the recorded data.

Seasonality of spider relocations.—In order to compare differences in spider relocation as a function of season, the same size classes were used as for the calculation of residence periods except that the Large spider size class was split into Medium and Large. Thus, Large in this context only contains adult and subadult females; these were split off because all adults die by winter and will therefore leave a web site. Data were extracted for each residency from the long-term observations at Waitara Creek—the season a spider moved into a position and its size, the seasons during which it was resident at a position, and the season and size at which it moved on (Smith 2006b). If a spider had grown between size-classes during its period of residence, the original data were examined to separate the seasons in which the two different size classes were present. For each kind of move, in or out, and for each size class of spider, the total number of moves per season was calculated as a proportion of the numbers of spiders in that class recorded during the season.

RESULTS

Short-term observations of residence time.—The residence period through each short-term transect period is 24.9 nights, averaged over all three sites. Per site the averages are: Myall, 26.3 nights; Waitara Creek, 23.5 nights; West Head, 23.9 nights. The presence of individual spiders through the recording period at each site is depicted in Fig. 2. All spiders were used for the calculations, which therefore include movements due to conspecific interference.

Long-term observations of residence time.—The mean residence time for all spiders is 4.80 recording periods (40.75 days), SD = 5.57, $n = 218$. The longest recorded residence is 31 recording periods (approximately 263 days) (Fig. 3a). When Small and Large residence times are compared, the distribution of residence times is found to be significantly different between the two size classes ($P = 0.012$). The mean residence times are 3.77 sampling periods, (32 days), for Small spiders (SD = 4.51, $n = 138$), and 6.59 sampling periods (56 days), for Large spiders (SD = 6.69, $n = 80$). Most aggregated spiders were omitted in calculating these figures; hence movements due to conspecific interference are minimal.

The distribution of residence times of Small spiders is significantly different from the random hypothesis ($0.05 > P > 0.025$) (Fig. 3b). This is not the case for the Large spiders; the distribution of residency times for these is not significantly different from random ($0.5 > P > 0.1$) (Fig. 3c). For the complete data set see Smith 2006b.

Seasonality of spider relocations.—Summer and autumn are shown to be the peak seasons for beginning a period of residence (Table 2a); spring and summer are the peak seasons for leaving (Table 2b). Winter is a period of relatively low mobility, at least for spiders arriving into a new web site.

DISCUSSION

The average residence time of 24.9 nights for *P. noblei* (spiders of all instars) in the short-term observations is just slightly shorter than the residence time of adult females of *Cyclosa octotuberculata* Karsch 1879 (26.3 days, Nakata & Ushimaru 2004). The residence time of a wide variety of spiders is shown in Table 1 in order of increasing length, and both of these species fit in towards the bottom of the table, i.e. they have long average residence periods. The figures for *Poltys* were calculated in a similar way to the majority of the

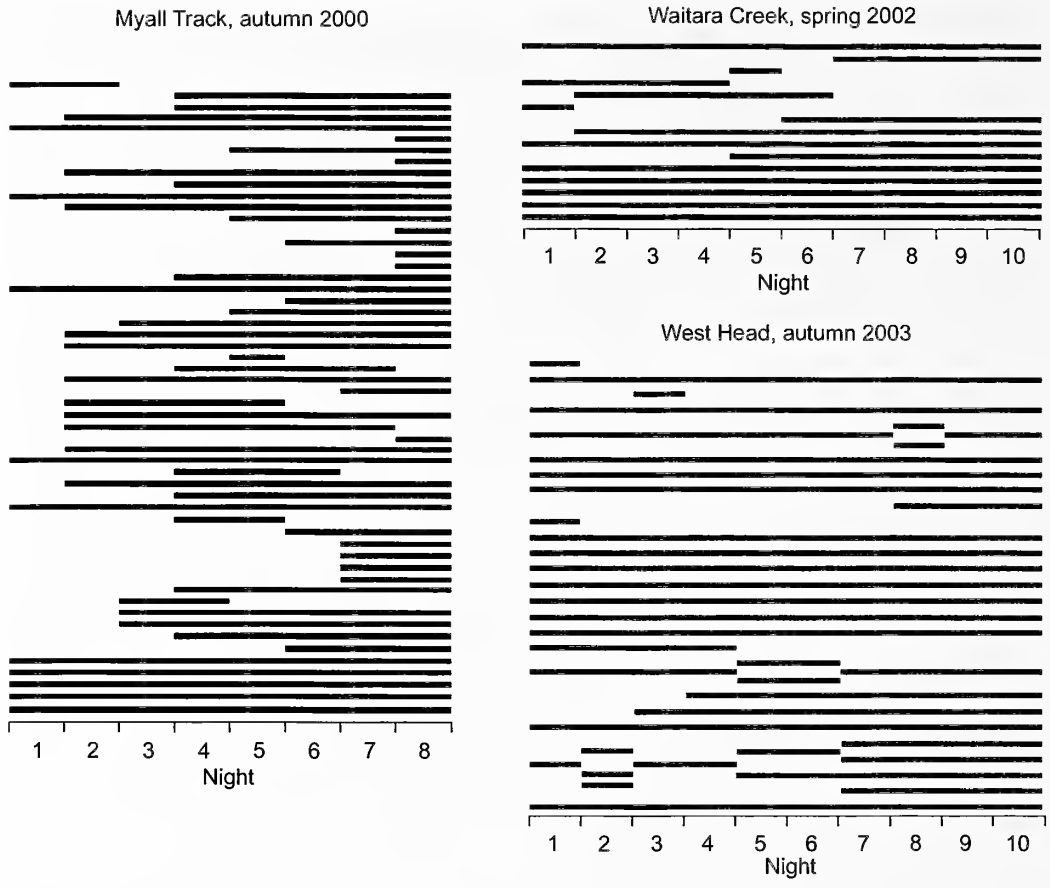

Figure 2.—Spider presence at Myall, Waitara Creek and West Head short-term transects. The length of each bar represents the presence of a particular spider through one or more nights. Spiders ordered as positioned along transect route, nearest axis at start.

species shown here, from the rate of departure of spiders from web sites over several consecutive nights of observation. The major difference between the short-term results for *Poltys* and most of the other studies included here is the wide range of instars represented in the current studies and the inclusion of some spiders known to have experienced interactions with conspecifics. The overall figure from the long-term transects (all ages) is rather longer at 40.75 nights and is only second to the residence times of *N. clavipes* spiderlings among the silk recycling species in these examples. These *Nephila* were protected from predators in enclosures and provided with abundant prey, however, which is hardly a natural situation, and there are similar caveats for the long-term transect results for *Poltys*, discussed below. *Nephila clavipes* and *P. noblei* (Large spiders), have been shown to have an essentially random pattern of relocation from web sites (Vollrath & Houston 1986; Smith this paper); the pattern of relocation of the other orb web species at the bottom of the table has not been tested. These characteristics of long residence period and random relocation pattern suggest some hidden high cost of moving may be present for each species in comparison to the presumed freely moving spiders at the top of Table 1.

The risk of predation, or expenditure of energy associated with avoiding such a fate, has previously been suggested to be this hidden cost for the diurnal species with long residence periods. For *Nephila* there is a direct risk after relocating due to the lack of protection usually afforded by an extensive barrier web (labyrinth) at an established site (Vollrath 1985). In the case of *C. octotuberculata*, the spider hides among debris and egg sacs that are incorporated in a line across its web. The line of debris is taken by the spider when it relocates and although this protects the spider after arrival at a new site, carrying such a burden takes more energy and time (Nakata & Ushimaru 2004). In the same study *Cyclosa argenteoalba* Bösenberg & Strand 1906 was compared with *C. octotuberculata*. This species does not use debris for camouflage in the web and correspondingly was found to have a much shorter average residence time (Table 1). Even in certain spiders that do not recycle web proteins, predation during relocation has been found to be a major cost that favors long residence periods. Only 60% of desert widow spiders, *Latrodectus revivensis* Shulov 1948, survived relocation, far outweighing the material cost due to loss of silk (Lubin et al. 1993).

Like the desert widow spider mentioned above, the remaining orb web species with long residence times, *P. noblei* and *Tetragnatha elongata* Walckenaer 1842, are primarily nocturnal. Nocturnally active spiders largely avoid the dangers of being exposed in a web by day, but still require a strategy to avoid predation during this time while the majority of predators are active. Some, like *L. revivensis*, hide in a retreat that may offer a physical barrier against some predators as well as concealing the spider; other taxa, such as these *Poltys* and *Tetragnatha* Latreille 1804 species, rely on camouflage. This camouflage is manifested both in coloration and shape. *Tetragnatha* are elongate and usually lie on vegetation with legs extended linearly, blending in with the

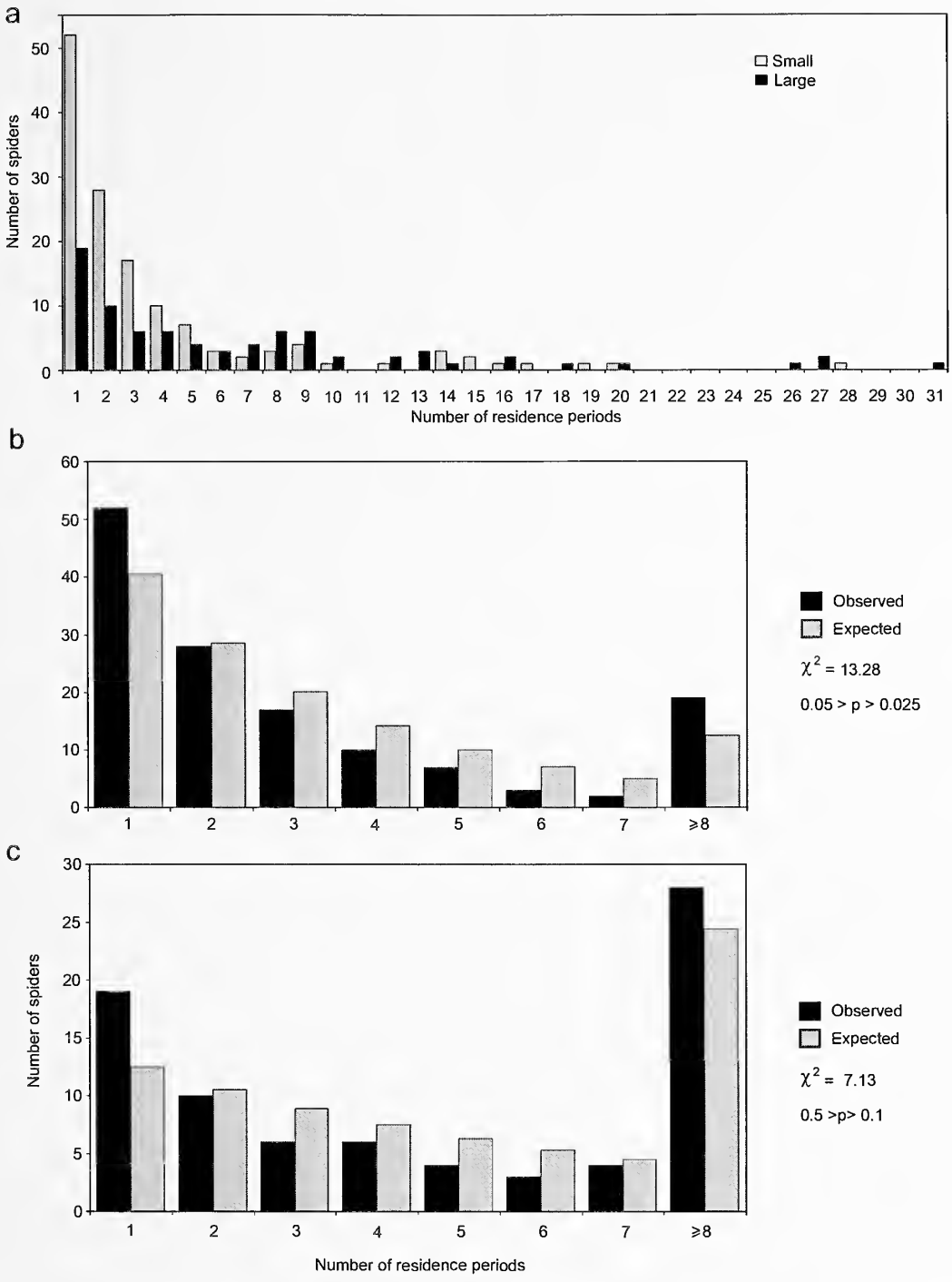

Figure 3.—The frequency of occurrence of spider residency periods: a. Small compared to Large spiders; b. histogram of residency periods of Small spiders (tail values pooled) compared to a random hypothesis; c. ditto for Large spiders. Calculations in both 3b and 3c use 6 degrees of freedom because two parameters of the expected series are derived from observed values (details in Smith 2006b).

twig or leaf, while *Poltys* sit on the side or end of a twig with legs tucked in, appearing like a broken twig end or a dead leaf bud. Voluntary relocation would take place during the night, so one cost is loss of foraging time. But for these spiders the main danger in moving from a known "safe" web site may be the risk of not matching the substrate at a new, unknown, site and thereby becoming easily visible to a predator.

Movement strategies of spiders in different age classes are provided by the long-term results of the present study (Figs. 3a–c) and the seasonal analysis (Tables 2a, b). For *P. noblei*, the non-random pattern of residence of Small spiders compared to the apparently random pattern of Large spiders suggests that the risk associated with relocation increases as spiders become larger and thus more reliant on effective camouflage. Such changes in foraging patterns with age due to changing costs were predicted by Janetos (1982b). This changing relationship between efficient foraging for growth and the need for camouflage can also be seen in the seasonal shift in moves in and out of web sites. For *P. noblei* a general strategy is to move in spring and summer when rapid growth is

Table 2.—The percentages of spiders which move on a seasonal basis, classified by spider size. A. Spiders beginning residency (moving in); B. Spiders ending residency (moving out). The number of spiders in size classes differs due to specimens which grow from one size class to another during their period of residence. Large = adult plus subadult females; Medium = all other juvenile females; Small = juvenile males and females too small to sex (up to about 3 molts).

A.

Moving IN % (n_{move})

Spider size class	Winter	Spring	Summer	Autumn
Large	100 (3)	83 (10)	69 (9)	100 (1)
Medium	30 (6)	63 (17)	87 (13)	81 (21)
Small	45 (9)	62 (13)	100 (85)	67 (31)
All spiders	42 (18)	67 (40)	95 (107)	73 (53)

B.

Moving OUT % (n_{move})

Spider size class	Winter	Spring	Summer	Autumn
Large	50 (1)	86 (12)	93 (14)	100 (2)
Medium	68 (13)	88 (22)	77 (10)	54 (15)
Small	56 (10)	100 (20)	85 (68)	78 (31)
All spiders	62 (24)	92 (54)	85 (92)	69 (48)

occurring, but by autumn many spiders are settling into sites where they will remain until spring (Tables 2a & 2b). Spring is a time of high mobility in all size classes. In fact, 100% of Small spiders end their residence during spring, even though only 60% begin a residence during this period. The 40% discrepancy in numbers will be largely due to the maturation of males. Other size classes also show a high percentage of spiders moving out of established web sites (i.e., ending a period of residency) in spring. This may be to seek a prey-rich web site after a long period of low prey availability over winter. Indeed the model of Leclerc (1991) based on observations of the linyphiid *Tenuiphantes flavipes* (Blackwall 1854) predicted differential optimal strategies with regard to staying or moving dependent upon the spiders' body fat reserves. So many spring movements could also indicate that staying too long carries risks that balance the dangers of moving. Predators may learn to associate a build up of silk lines with the likely presence of spider prey. For instance, it is often unclear what cue initiates the cryptic prey flushing behavior reported in *Sceliphron laetum* (F. Smith) (Coville 1987), a technique observed in the capture of *Poltys* spiders by this wasp (R. Raven pers. comm.).

The long-term figures for *Poltys* residence times are overestimates to some extent. In particular, many spiders may have been missed because they both arrived and left a web site between samples and this factor would make the long term average residence period more comparable with the figure from the short-term studies. Another factor that accounts for some of the difference between long-term and short-term average residence periods is the omission of spiders that were in aggregations from the former. Nevertheless, many of the studies listed in Table 1 also excluded moves caused by conspecific interactions, so this does not affect the within-table comparison. Finally, the life history of *P. noblei*, which often extends over more than one season, leads to the inclusion of winter records in the long term averages. Winter is a season of low general mobility and was not sampled in any other study listed in Table 1. Therefore, it can be seen that a realistic figure for the average residence period for *P. noblei* that is comparable to other studies lies somewhere between the short-term and long-term results reported here. Nevertheless, the long-term results provide information on maximum stays, the distribution of residence times, and some information on differences between spiders of different ages. In fact the single longest recorded stay of *P. noblei*, of approximately 263 days, seems remarkable for a silk recycling species. Unfortunately this cannot be compared to other species both due to the "snapshot" nature of most studies and due to the differing life-histories. All other species examined are essentially univoltine and this time period would have covered the entire life-cycle from emergence; for this *P. noblei*, however, this period accounted for approximately two-thirds of its growth, the record covering it from the small end of Medium, through to adult, probably around five instars.

An attraction for web sites with conspecific silk has been demonstrated in at least one orb web species (Schuck-Paim & Alonso 2001) which might indicate the further possibility of overestimation of the period of web site tenacity of *Poltys* if web site take-overs occurred frequently. This error is most likely to occur among records for smaller specimens that were not individually distinctive and so I excluded aggregated spiders from the long term data if I became unsure about which spider was which at any time through the study. If present to a significant degree this error would be indicated by longer web site residencies for Small spiders than those of Large spiders, which were more recognizable as individuals. Instead the Small specimens show the most frequent movements, which is in agreement with the findings of other studies shown in Table 1. The lengths of some residence periods were further corroborated by observations of distinctive individuals that were using easily visible day-time hiding positions. Nevertheless, the spatial distribution of specimens in some cases, especially spiderlings, and reuse of sites, did suggest that *P. noblei* may be attracted by conspecifics, and/or that web sites were limiting. In the habitats where I found *Poltys* commonly, as in the areas where these studies were carried out, there were many more apparently suitable web sites than spiders. However the significance of spider spatial distribution was not tested here because of the complications of habitat heterogeneity, wind currents, and the structural suitability of different plant species for the webs and hiding places for spiders of different sizes.

The paucity of studies on nocturnal orb web spiders to some extent reflects the inconvenience of working odd hours, but nocturnal spiders may also make less ideal models than diurnal species due to differences in behavior. Diurnal species normally construct the new web within the frame of the previous one (e.g., Hodge 1987a). Thus, with no disturbance, the web will be in exactly the same place and repeated occupancy can be assumed to be a direct measure of the suitability of the web site for the spider. In contrast, nocturnal spiders such as *Poltys*, may spend up to 17 hours each day without a web, leaving in place only the bridging line, which is easily broken, and access lines between and along twigs. Except in an extremely simple structural situation, or in calm

weather, the position of the web is therefore unlikely to be exactly replicated from night to night. In the observations reported here, I discounted small changes in web sites, as did, for example, Enders (1975) in the studies listed in Table 1 and possibly others who did not report on the precise details. However, in a habitat where supports are widely separated, even the relocation of a single support line may significantly change the web position and so could be considered as relocation (e.g., Nakata & Ushimaru 2004). Such heterogeneity in recording protocol and in spider behavior makes detailed comparisons between studies difficult. Nevertheless trends do emerge from this range of data and, in particular, the new data on *Poltys* add support to the findings of previous authors who suggested the connection between long residencies, random patterns of movement, and a high cost of relocation due to predation risks. Among the species with long web site residence times the precise *modus operandi* of the threat differs between the two diurnal species, *N. clavipes* and *C. octotuberculata*, but the requirement for effective camouflage may well be the key factor for both of the nocturnally active, diurnally cryptic species, *T. elongata* and *P. noblei*. Despite presenting interesting challenges, nocturnal and/or cryptic spiders provide useful insights into otherwise hidden facets of predator prey interactions.

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Spiderling emergence in the tarantula *Grammostola mollicoma* (Ausserer 1875): an experimental approach (Araneae, Theraphosidae)

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Abstract. The ability of *Grammostola. mollicoma* (Ausserer 1875) spiderlings (Araneae, Theraphosidae) to emerge from the cocoon without the assistance of their mother was tested experimentally. We created two experimental groups with 23 cocoons in each group. In one of the groups we cut the cocoon wall creating an opening; in the other group, the cocoon remained untouched. We found no differences between the groups in either the number or instar composition of the spiderlings that emerged. The spiderlings were able to emerge without the assistance of their mother. The emerging instars in both groups were precocious compared to previous suggestions in the literature.

Resumen. Ponemos a prueba experimentalmente la capacidad de *Grammostola mollicoma* (Ausserer 1875) (Araneae, Theraphosidae) para salir de la ooteca sin asistencia de su madre. Creamos dos grupos experimentales cada uno con 23 ootecas. En uno de los grupos cortamos la pared de la ooteca mientras que el otro permaneció intocado (grupo control). No encontramos diferencias en el número de arañitas emergidas ni en los estadios de emergencia entre los grupos. Los hijos pudieron emerger sin la asistencia de su madre. Los estadíos en que las arañitas emergieron en ambos grupos fueron levemente más precoces que lo indicado previamente en la literatura. Se discuten posibles explicaciones para estos resultados.

Keywords: Cocoon-opening, mother assistance, emergence-instars

Once spiders hatch from their eggs, they usually molt one or more times inside the cocoon or egg sac before they emerge. Although cocoon care and postembryonic development in spiders have been thoroughly studied, spiderling emergence is only known from a few observations, mainly in Araneomorphae (Eason 1964; Engelhard 1964; Fujii 1978; Vannini et al. 1986; Riechert & Jones 2001; Kürpick 2000; Viera et al. 2007 a & b). The mother's assistance is indispensable for the emergence of juveniles from the cocoon in lycosids (Fujii 1978; Higashi & Rovner 1975), in the subsocial theridiid *Anelosimus* cf *studiosus* (Viera et al. 2007b), and in the eresid *Stegodyphus lineatus* (Latreille 1817) (Schneider and Lubin 1997). In these species, spiderlings are unable to open and exit the egg sac by themselves and die if the mother does not open it. In contrast, in other Araneomorphae like orb weavers, where the mother dies a few days after building the cocoon, the spiderlings are capable of emerging even in her absence (Foelix 1996).

In mygalomorphs, Coyle & Icenogle (1994) suggested from indirect evidence that spiderlings of the antrodiaetid *Aliatypus* spp. may need the mother's assistance to emerge, while Marechal (1994) observed that spiderlings of the diplurid *Ischnotele guianensis* (Walckenaer 1837) are able to hatch by themselves from the cocoon without external help. No other reports about spiderling emergence are available for most mygalomorph families.

Members of the family Theraphosidae are usually large and long-lived and in the last decades they have become popular as pets in many countries. Although several papers report different aspects of their biology (Petrunkevitch 1911, 1934; Baerg 1928, 1958; Gerhardt 1929, 1933; Bucherl 1952; Melchers 1964; Galiano 1969, 1973a & b, 1984, 1992; Stradling 1978, 1994; Minch 1979; Celerier 1981; Kotzman 1990; Costa & Pérez Miles 1992, 2002; Pérez-Miles & Costa 1992; Marshall & Uetz 1993; Schillington & Verrell 1997; Huber 1998; Janowsky-Bell & Horner 1999; Locht et al. 1999; Punzo & Henderson 1999; Yañez et al. 1999), none describes spiderling emergence in detail. Although we observe mother care of cocoons and spiderlings in several theraphosids, including *Grammostola mollicoma* (Ausserer 1875), spiderling emergence remains obscure.

Usually the eclosion of the spider from the egg determines the transition from the embryonic to postembryonic life (Foelix 1996). However, the characteristics in which the spiders hatch varies in different species (Holm 1940; Vachon 1957; Peck & Whitcomb 1970; Ramousse & Wurdak 1984), contributing to a confusion in the terms and descriptions of developmental instars in spiders (Foelix 1996). As Galiano has provided a comprehensive study of theraphosid development (1969, 1973a & b, 1984), we followed her terms and concepts. Using her terms, instar A is the 1st intrachorional state and consequently instar B is the first instar out of the egg. Although in instar B the spider is completely free of the egg, the body is bent and the legs are extended but do not contact with substratum and are not functional for locomotion. In addition, the eyes and several kinds of setae are absent. These instars as well as instars C and D are completed within the cocoon in *Grammostola pulchripes* (Simon 1891). More intra-cocoon instars and less development in the early instars was considered as a derived characteristic for Theraphosidae in comparison with other mygalomorphs (Galiano 1969).

In this study we experimentally tested if spiderlings of the theraphosine *G. mollicoma* are able to emerge from cocoons without the assistance of their mothers. We additionally compared the instars of emergence with predictions from previous postembryonic studies (Galiano 1969, 1973), discussing their possible adaptive value.

METHODS

We used 46 cocoons of *G. mollicoma* (northern form) obtained through the Uruguayan mail and confiscated from illegal trade. All were presumably collected at a site near Achar, Tacuarembó, Uruguay [32°23′60″S, 56°04′57″W] con-

Table 1.—Number of cocoons and distribution of instars in which spiderlings emerged in treatment and control groups. See methods for explanation of abbreviations for different instars (C–E).

Instars of emerged spiderlings	C	C + D	D	E	D + E	Not registered
No. of Cocoons Treatment group	2	0	6	2	8	4
No. of Coeoons Control group	0	1	3	1	12	3

sidering police evidence, habitat description and known distribution of this species. In addition, 800 adults of *G. mollicoma* were simultaneously confiscated in another mailing by the same person from the same locality.

Cocoons were maintained in plastic containers (83 mm diam. × 105 mm high). Observations took place from 24 January to 7 March 2007. We divided the cocoons into two experimental groups with 23 cocoons in each one. In one of these groups (treatment group) we made a cut 5 mm long with scissors in the cocoon wall on the first day of observation (this cut was approximately of the same size as natural orifices made by spiderlings); in the other group (control), the cocoons remained closed. During the experimental period the room temperature varied between 26.6 ± 1.4° C and 24.2 ± 1.4° C, and photoperiod was natural (approximately 14 h day:10 h night).

We examined the cocoons daily to monitor the spiderlings's emergence. When the spiderlings emerged, we counted them and determined the postembryonic instars (following Galiano 1969). Instar A is the last intracorional instar and B is the first extracorional instar; we did not observe these instars in our study. Instar C characteristics include: bent body, absence of body pigments, absence of eyes (only maculas), legs not completely functional. Instar D has cephalothorax and abdomen in the same plane, pigments present, eyes present, absence of tarsal scopulae and claw tufts, slow locomotion. Instar E shows body densely hirsute, scopula and claw tufts present and normal locomotion. When more than 50 spiderlings emerged, the remaining progeny was preserved in ethanol and examined, the cocoon was measured (major and minor axis) and its natural openings were counted. At the end of the experiment, the cocoons that remained closed were opened and examined. Voucher spiderlings and opened cocoons were deposited in the arachnology collection of Facultad de Ciencias, Montevideo, Uruguay.

RESULTS

Spiderlings successfully emerged from 22 cocoons in the treatment group and 19 in the control group (non-treatment). No significant differences were found in the frequency of spiderling emergence between groups ($X^2 = 2.02$, $P = 0.15$). The mean number of spiderlings born alive per cocoon in the treatment group was (mean ± SD) 91.5 ± 46.8 and in the control 102.0 ± 38.4, again with no significant differences between groups ($t = 0.78$, $P = 0.45$).

The spiderlings emerged from their cocoons in instars C, D, and E, both in the treatment and control groups. Very few spiderlings emerged in instar C: one and six from each of two cocoons of the treatment group and one from a cocoon of the control group. Curiously, in some cocoons spiderlings emerged simultaneously in two different instars (Table 1). No additional teeth on the chelicerae nor bifurcated cheliceral tips or other structures related to cocoon opening were found in the emerged spiderlings. Table 1 shows how the pattern of instar emergence was distributed among the cocoons. The distribution of mean numbers of spiderlings emerged in instars D and E by cocoon group are shown in Fig. 1. All the spiderlings that emerged in instar D molted to instar E within 24 h after emergence.

Of the four cocoons from which spiderlings did not emerge, we found eggs infected with fungus in two of them, dry eggs in another, and nine spiderlings alive (three of them molting), seven dead, and several unhatched eggs in the last cocoon.

The period from the beginning of the observation to the emergence of spiderlings from the cocoons took 12.9 ± 8.2 days in the treatment group and 10.1 ± 5.9 days in the control group, with no significant difference between these periods ($t = 1.25$, $P = 0.23$).

Cocoons averaged 43.3 ± 6.8 mm and 39.6 ± 7.4 mm (major and minimum axes) in the treatment group and 43.8 ± 5.8 mm and 41.6 ± 5.8 mm in the control group, showing no significant differences in cocoon size between the groups (major axis: $t = 0.28$, $P = 0.78$; minimum axis: $t = 0.96$, $P = 0.34$). The number of natural perforations, if we do not consider the experimental cut, was 0.55 ± 0.60 in the treatment group and 1.53 ± 0.61 in the control group. Significant differences were found between groups ($t = 5.19$; $P < 0.0001$).

DISCUSSION

Our results clearly showed that spiderlings of *G. mollicoma* are able to emerge from the cocoon without the assistance of their mother as was reported by Marechal (1994) for the diplurid *I. guianensis*. Coyle & Icenogle (1994) did not observe

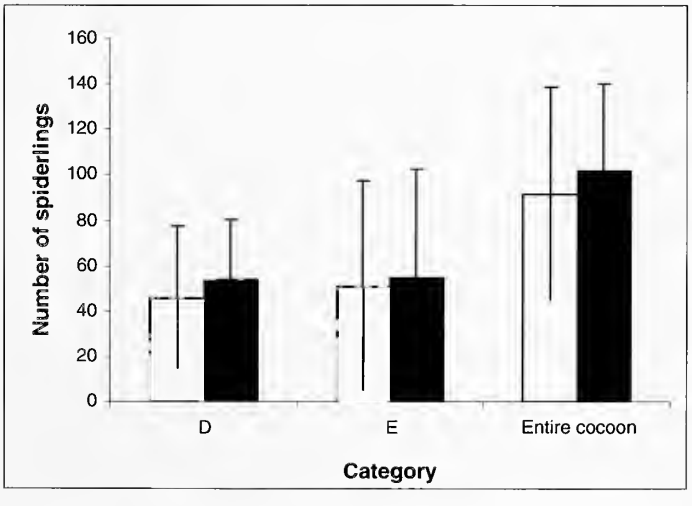

Figure 1.—Means and standard deviation of spiderlings emerged in instars D, E and of total occurrence of spiderlings alive per cocoon (including those that remained inside the cocoon). The treatment group is represented in white and the control group in black.

Table 2.—Reports of number of spiderlings * or eggs per cocoon and cocoon size in Theraphosidae taken from the literature.

Species	Number of spiderlings * or eggs	Cocoon Size (major axis)	Author
Avicularia avicularia	103–145 *	-	Stradling 1994
Avicularia metallica	178–182	-	Charpentier 1992
Avicularia versicolor	12–221	-	Charpentier 1992
Pachistopelma rufonigrum	30, 30 *	-	Dias & Brescovit 2003
Acanthoscurria gigantea	600	-	Ibarra Grasso 1961
Aphonopelma chalcodes	454–555	-	Minch, 1978
Aphonopelma hentzi	206–911	-	Punzo, 1999
Aphonopelma joshua	51 *	12 mm	Prentice 1997
Ceropelma longisternale	16–111	-	Costa et al. 1992
Dugesiella crinita	800–1000	-	Baerg 1958
Dugesiella hentzi	500–1000	-	Baerg 1958
Euathlus smithii	> 700	-	Clarke 1991
Eurypelma californica	621–1018	-	Baerg 1938
Grammostola burzaquensis	100–120	30 mm	Ibarra Grasso 1961
Grammostola mollicoma		43.5 mm	this study
Phamphobetus roseus	1200	-	Ibarra Grasso 1961
Theraphosa blondi	36, 44 *	60 mm	Lambert & Dupre 1992
Theraphosa blondi	78 ± 5.57	-	Marshall & Uetz 1993

direct evidence for the mother's assistance in the antrodiaetid *Aliatypus* spp. Their indirect observations provided weak support for the hypothesis that the mother's help is required. The small number of natural perforations found in the cocoons of the treatment group suggests that spiderlings could utilize pre-existent holes.

Copulation during egg sac care was reported recently for this species (Postiglioni 2007). The ability of spiderlings to emerge without assistance might be an important trait that permits the mother to be receptive and exposed to the risks (i.e., predation) of courtship and copulation without jeopardizing the success of her spiderlings.

The mean number of spiderlings per cocoon (or clutch) for *G. mollicoma* was moderately low in comparison with most Theraphosidae (Table 2). This characteristic could be interpreted as plesiomorphic if compared with the sister family Barychelidae with 20–80 eggs (Raven 1994). Other theraphosids as *Aphonopelma joshua* Prentice 1997, *Plesiopelma longisternale* (Schiapelli & Gerschman 1942), *Theraphosa blondi* (Latreille 1804) and some avicularines share with *G. mollicoma* a low clutch size.

Galiano (1969) observed a bifurcated tip on the cheliceral fang in instars B and C of *G. pulchripes* (in synonymy with *G. mollicoma* by Pérez-Miles et al. 1996), which we found to be absent in instar C of *G. mollicoma*. Galiano also indicated the presence of maxillary cuspules and the scarcity of hairs on tarsi and tibiae in instar C of *G. pulchripes* but we found no such cuspules and several tibial and tarsal hairs, which causes us to question the synonymy of these species. The absence of special structures in spiderlings related to cocoon opening suggests that they open the cocoon with the chelicerae. The experimental perforation seemed not to affect the normal development of the cocoons nor the number of spiderlings born alive, considering the absence of significant differences between the groups. Instar C seems to be a pre-emergence instar because few individuals emerged in this instar, and only in the treatment group. The absence of eyes and pigments and the bent body, which impedes locomotion (Galiano 1969), also agree with a pre-emergence instar.

Galiano (1969) incubated isolated eggs of *G. pulchripes* outside the cocoon, and based on morphological evidence during development, proposed that spiderlings emerge in instar E. Our results partially agree with this author because we found that half of *G. mollicoma* spiderlings emerged in instars D, molting to E outside the cocoon within about 24 h. The emergence in two different instars also indicates a slight asynchrony of molting between instars D and E. However, instar E seems to be the first in which the spiderlings are independent enough and ready for their free life (Galiano 1969). Instar E is the first instar where urticating hairs develop (Pérez-Miles 2002) and the spiderlings are able to feed by themselves (occasional observations). It is not clear what the advantages are for the spiders to emerge in the precocious instar D. Probably in this instar spiderlings are not able to open the cocoon by themselves and instead use the openings made by spiderlings in instar E to emerge. Prentice (1997) reported that spiderlings of *Aphonopelma joshua* Prentice 1997 emerge in the fourth or fifth instar probably homologous with D and E, which is similar to our findings in *G. mollicoma*.

Galiano (1969), following Holm (1956), indicated that a low quantity of yolk and an increased degree of organization in early extracorional instars imply a few number of instars intra-cocoon and a plesimorphic condition, as in *Telechoris striatipes* (Simon 1889) [(ex *Ischnothele karschi* (Bösenberg & Lenz 1895)]. Galiano (1969) has stressed the importance of having four instars intra-cocoon in *G. mollicoma* and consequently considered this characteristic as derived in comparison with most mygalomorphs and other Araneae. For example the Mesothelae *Heptathela kimurai* (Kishida 1920) and other mygalomorphs such us *Atypus karschi* Dönitz 1887 and *Telechoris striatipes*, have only two or three states intra-cocoon (Yoshikura 1952, 1958 and Holm 1956; cited by Galiano 1969). In *H. kimurai* and *T. striatipes*, spiderlings have two instars inside the cocoon while *A. karschi* has three. Stradling (1994) reported only one intra-cocoon postembryonic instar in *Avicularia avicularia* (Linnaeus 1758), which seems to be a record in Theraphosidae. Our findings in *G. mollicoma* with three instars intra-cocoon question the indirect

evidence of Galiano (1969) and consequently the evolutionary interpretation of Galiano.

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Dragline deposition patterns among male and female *Hogna helluo* (Araneae, Lycosidae) in the presence of chemical cues from prey

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Abstract. Prey are able to show adaptive antipredator responses in the presence of silk from the wolf spider *Hogna helluo* (Walckenaer 1837). *Hogna helluo* also is attracted to chemical cues associated with previously consumed prey. Consequently *H. helluo* may benefit by modifying its silk deposition when encountering prey cues to avoid detection. Silk is an important medium for female wolf spiders to attract prospective mates, whercas silk is putatively less important for males to attract females. Females also consume much more food than males after maturity; therefore, male and female *H. helluo* may differ in the relative costs and benefits of silk deposition with respect to improved feeding efficiency. We tested whether field-caught male and female *Hogna hellno* changed silk deposition patterns in the presence of excreta deposited by domestic crickets, *Acheta domesticus*, (Linnaeus). Hungry male and female *H. helluo* were allowed to deposit silk for four hours in containers either previously occupied by five crickets for 24 h or devoid of cues ($n = 36$). We found no significant decrease in silk dragline deposition among males or females in the presence of prey cues; however, female spiders showed a significant decrease in the number of attachment disks produced in the presence of cricket cues whereas males did not. Our results suggest that *Hogna helluo* do change silk deposition patterns in the presence of crickets, but that these changes are sex-specific.

Keywords: Draglines, anti-predator, crickets, kairomone, wolf spider

All species of spider putatively produce silk draglines as they move through their environment. These threads serve as an important communication medium among spiders (reviewed by Schulz 2004; Huber 2005; Gaskett 2007). Some species discriminate between conspecific and heterospecific silk (Roland 1984). Others are able to assess fighting ability (Clark et al. 1999) or mating status of conspecifics using only information associated with draglines (Rypstra et al. 2003; Schulz 2004; Roberts & Uetz 2005).

Draglines from the major ampullate glands may potentially be an important source of information for both predators and prey of spiders (Schulz 2004). Recent studies have found that the wolf spider, *Pardosa milvina* (Hentz 1844), is capable of extracting information about predator risk via silk and other metabolic products from a larger co-occurring wolf spider, *Hogna helluo*. From chemical cues alone, *Pardosa milvina* can extract information about size (Persons & Rypstra 2001), diet (Persons et al. 2001), and hunger level (Bell et al. 2006) of *H. helluo* as well as how recently it has been in the area (Barnes et al. 2002). This information is then used to effectively avoid predation by *H. helluo*. Similarly, spiderlings of *Rabidosa rabida* (Walckenaer 1837) reduce activity and show avoidance behavior when encountering silk of adult female *P. milvina* (Eiben & Persons 2007). A number of insect species are also capable of detecting silk and other cues associated with spiders and responding with antipredator or avoidance behavior. Japanese beetles (*Popillia japonica* Newman 1841) and Mexican bean beetles (*Epilachna varivestis* Mulsant 1850) reduce herbivory on soybeans previously walked on by the wolf spiders *H. helluo*, *Rabidosa rabida* (Walckenaer 1837), or *P. milvina* (Hlivko & Rypstra 2003) and the field cricket, *Gryllus integer* (Scudder 1901) reduces activity and avoids substrates containing chemical cues associated with the funnel-web spider *Hololena nedra* (Chamberlin & Ivie 1942) if *H. nedra* have previously fed on *G. integer* (Kortet & Hedrick 2004).

Given that spider silk and other metabolie products are known to be used by prey to alert them to the presence of a predator, it may be adaptive for spiders to modify silk deposition during foraging if they are capable of detecting and responding to chemical cues associated with prey. A number of spider species are capable of detecting and preferentially foraging in areas where chemical cues or metabolic waste products from prey are found. The wolf spider *Hogna helluo* shows a marked preference for substrates previously occupied by crickets or the smaller co-occurring wolf spider, *Pardosa milvina* (Hentz 1844), when previously fed crickets or *P. milvina* respectively (Persons & Rypstra 2000). Similar diet-based preferences for substrates with prey cues have been found in the wolf spider *Hogna carolinensis* (Walckenaer 1805) (Punzo & Preshkar 2002), *Trochosa parthenus* (Chamberlin 1925), and the oxyopid, *Oxyopes salticus* (Hentz 1845) (Punzo & Kukoyi 1997). The zoodariid ant-specialist, *Habronestes bradleyi* (Cambridge 1869) is attracted specifically to the alarm pheromones of the meat ant *Iridomyrmex purpureus* (Smith 1858) (Allan et al. 1996) and the wolf spider *Schizocosa ocreata* (Hentz 1844) is attracted to substrates previously occupied by the cricket *Acheta domesticus* (Persons & Uetz 1996).

Since adults of the wolf spider, *H. helluo*, are known to change foraging behavior when detecting prey chemical cues and prey show antipredator responses when detecting substrates with *H. helluo* silk, we hypothesized that *H. helluo* should modify their silk deposition when detecting chemical cues from prey. However, the relative fitness trade-offs for modifying silk deposition while foraging may be different for males and females. Adult female *H. helluo*, like most lycosids, are larger, more rapacious, and gain weight quickly relative to males (Walker & Rypstra 2001; Lehmann et al. 2004). Therefore, females benefit more by improved foraging

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efficiency (Walker & Rypstra 2002). However silk may also be used by females to advertise to males their willingness to mate and, thus, there may be an opportunity cost associated with stopping silk deposition among females but not males. Here we compared changes in silk deposition of adult male and female *H. helluo* when detecting chemical cues associated with prey and predicted that females would show a greater shift in silk deposition behavior than males. If cricket antipredator responses to spider silk are especially effective, females should dramatically reduce silk production when encountering cricket chemical cues. Alternatively, if females use silk to mark and subsequently navigate around foraging patches likely to contain prey and prey responses to silk are weak, then females should increase silk deposition when detecting prey cues.

METHODS

Spider collection and maintenance.—Male and female *Hogna helluo* were collected in agricultural fields in Snyder County, Pennsylvania. Spiders were housed individually in 9 cm diameter, 7 cm high opaque containers. Each container was filled with 2–3 cm of moistened peat moss that served as a water source and means of maintaining humid conditions within the container. To familiarize spiders with cricket prey and minimize the effects of prior feeding experiences on silk deposition responses, spiders were fed weekly 2–3 domestic house crickets, *Acheta domesticus* (L.) for 3 wk prior to testing. Water was added to containers ad libitum to maintain a moist environment.

Substrate and trial container preparation.—Sheets of paper were prepared as substrates prior to testing. Each sheet was printed with an 80 mm diameter circular grid. Each paper substrate was prepared by printing a white on black alphanumerically coded 2.5 mm grid pattern onto each sheet of standard copy paper. These grids were cut out and stored until use in an air tight container. Latex gloves were worn and scissors were wiped with ethanol to prevent contamination. Each grid was taped into a 9 cm diameter, 7 cm high opaque container.

Experimental design.—*Hogna helluo* spiders were fed 2–3 domestic house crickets once a week for 3 wk prior to testing. Ten days prior to the start of the experiment all food was removed and feeding was stopped until after testing. Water continued to be provided as needed. Spiders were randomly assigned to cricket cue or control groups in equal numbers. Containers in the cricket cue treatment were prepared by placing 5 adult male and female *Acheta domesticus* on prepared substrates for 24 h. Crickets were then removed and treatment spiders were transferred into testing containers using a plastic 166 ml (= 45 dram) vial. Control spiders were placed into prepared testing containers void of any cricket cues. After 4 h in testing containers, spiders were carefully removed so as to not disturb deposited silk. Spiders were returned to their respective housing containers. Returned spiders were then fed 2–3 crickets and all experimental procedures were repeated with individual spiders being switched between control and cricket-cued treatments. Results were analyzed using repeated-measures ANOVA with sex and prey cue as factors.

Silk quantification.—Testing containers were examined using a Meiji EMZ-5 Stereo microscope. Silk was quantified using two methods. Silk draglines were counted by the number of squares that were covered with 50% or more silk. We also counted the total number of attachment disks deposited on the gridded sheets.

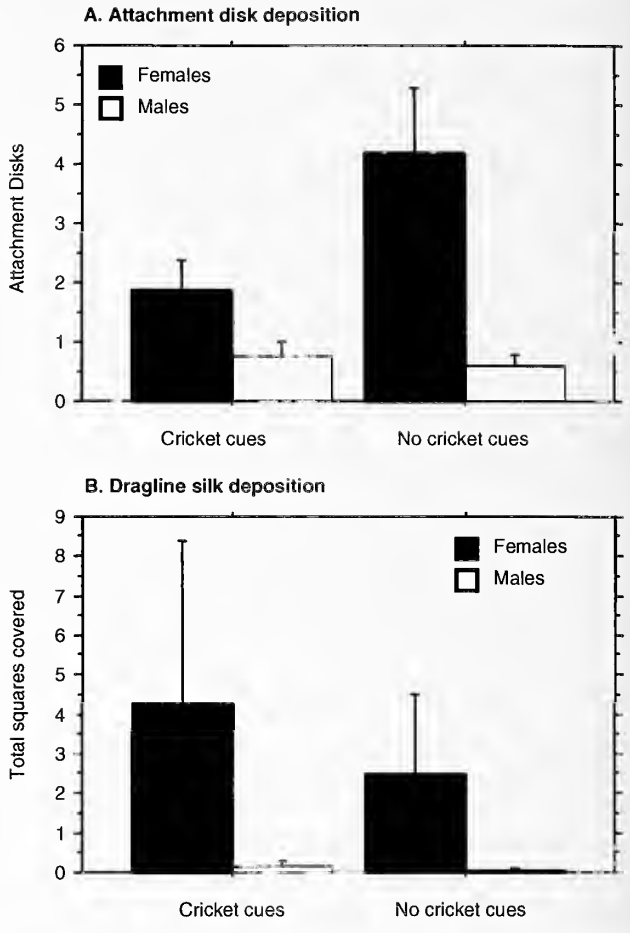

Figure 1.—A. Mean number of attachment disks deposited by male and female *H. helluo* (+ S.E.) while on clean sheets of paper (no cricket cues) or sheets of paper previously occupied by five crickets (*Acheta domesticus*) for 24 h (cricket cues). B. Total number of squares with at least 50% silk dragline deposition by male and female *H. helluo* (+ S.E.) while on clean sheets of paper (no cricket cues) or sheets of paper previously occupied by five crickets (*Acheta domesticus*) for 24 h (cricket cues).

RESULTS

We found a significant difference in attachment disk deposition between males and females (ANOVA: Sex = $F_{1,34}$ = 12.970 ; P = 0.001). We also found a significant effect of prey cue presence on attachment disk deposition (Repeated Measures ANOVA: Prey Cue = $F_{1,34}$ = 5.989 ; P = 0.0197) as well as a significant prey cue and sex interaction (Prey Cue * Sex = $F_{1,34}$ = 7.766 ; P = 0.0086; n = 36; Fig. 1A). Females produced about twice as many attachment disks as males while in the presence of prey cues and over four times as many in the absence of prey cues. Total quantity of dragline silk did not differ significantly by sex or the presence of prey cues (Repeated Measures ANOVA: Sex = $F_{1,34}$ = 1.453 ; P = 0.2346 ; Prey Cue = $F_{1,34}$ = 0.856 ; P = 0.3506 ; Prey Cue * Sex = $F_{1,34}$ = 0.713; P = 0.4045; n = 36; Fig. 1B).

DISCUSSION

Male and female *H. helluo* varied dramatically in the quantity of dragline and attachment disks deposited on the substratum. Females produced large amounts of dragline silk while males produced negligible amounts. Despite a seven-fold difference in mean dragline silk deposited by males and females, there was no statistically significant difference in the amount deposited. This is attributable mostly to high variability in female silk deposition behavior compared to males. Females also produced a greater number of attachment disks relative to males. The significant difference in attachment disk deposition between males and females may be the result of general differences in the role of silk in intersexual communication. The differences in deposition between sexes suggest that female *H. helluo*, like other lycosids, use dragline silk to attract males while males do not use draglines to attract females (reviewed in Schulz 2004). As originally predicted, our results indicate that males do not make any significant trade-offs between mate advertisement and compromised foraging within the context of silk production. Dragline silk deposition was highly variable among females. Attachment disks, produced by the pyriform glands of the anterior spinnerets (Dijkstra 1976), were often associated with fine gauge silk deposition, but it also appeared that females were capable of producing attachment disks in the absence of dragline silk. This suggests that attachment disks may have some function other than dragline fixation to the substratum. Dijkstra (1976) showed that male wolf spiders are capable of using attachment disks to gather information about the directional heading of females. If this finding is generally applicable to lycosids, attachment disk deposition by female *H. helluo* may be important in attracting males.

Our results are consistent with the hypothesis that females may reduce attachment disk deposition, but not dragline silk, to evade detection by prey. However there may be alternative explanations for this. Attachment disk reduction could be a by-product of reduced activity when encountering prey cues on a substrate. Female *H. helluo* activity drops dramatically when encountering substrates with cricket cues (Persons & Rypstra 2000) as might be expected from a sit-and-wait predator. When encountering cricket cues *H. helluo* typically switch to short bouts of walking and long periods of immobility relative to substrates without these cues. During pauses, *Hogna helluo* appeared to increase pivoting behavior on these cricket substrates, suggesting that the spiders were visually surveying the area for movement. If attachment disks are deposited primarily during pauses or stops after walking bouts, we would have expected increases in attachment disk deposition rather than decreases. Since it remains unknown if attachment disk and dragline silk deposition are tightly correlated to movement, we cannot eliminate the possibility that reductions in attachment disk deposition is a simple by-product of reductions in overall movement.

Acheta domesticus is an introduced species but has persisted in the eastern United States for some time (Blatchley 1920; Ghouri 1961). However *H. helluo* may not necessarily show as strong a behavioral response to chemical cues from it as the more common co-occurring species in central Pennsylvania, *Gryllus pennsylvanicus* (Burmeister 1838). *Hogna helluo* used in our study were fed a diet of *A. domesticus* for three weeks prior to testing. Previous studies have shown that this is sufficient time to induce a substrate preference for chemical cues associated with *A. domesticus* (Persons & Rypstra 2000) and thus enhance any foraging-related shifts in silk deposition.

It is currently unknown if *Acheta domesticus* display antipredator responses toward attachment disks and/or dragline silk, so it remains unclear if such shifts in silk deposition are adaptive. However other species of cricket do show adaptive antipredator responses to spider chemical cues (Kortet & Hedrick 2004), suggesting that *A. domesticus* may as well. Our results do not support the possibility that female *H. helluo* mark foraging areas likely to contain large numbers of prey by increasing silk deposition in areas with prey cues.

We did not measure shifts in defecation behavior in *H. helluo* but this too could be a significant source of chemical information for prey. The cricket, *Gryllus integer*, showed avoidance behavior of chemical cues from funnel-weaving spiders but only when these spiders were fed a diet of *G. integer*. Such diet-based information could originate from silk, excreta, or both. Morse (in press) found that adult female crab spiders, *Misumena vatia* (Clerck 1757), do not defecate near their hunting sites and selectively move to the distal portion of leaves when defecating. This could be done to limit attacks by parasitic wasps or parasites, but it may also reduce antipredator responses from insects that may respond to excreta from spiders.

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SHORT COMMUNICATION

Notes on two problematic eastern Asian species of the spider genus *Oecobius* (Araneae, Oecobiidae, Linyphiidae)

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Abstract. We address the current taxonomic status of two problematic Eastern Asian species of *Oecobius* Lucas 1846 and propose nomenclatural changes in view of the information currently available. *Oecobius formosensis* (Kishida 1943) is considered unrecognizable and proposed as a *nomen dubium*. Two synanthropic species, *Oecobius navus* Lucas 1859 and *Oecobius concinnus* Simon 1893, are newly recorded for Taiwan. Evidence from the literature indicating that a third species (*Oecobius marathaus* Tikader 1962) also occurs in that country is provided. *Oecobius sapporense* Saito 1934 is transferred to the genus *Neriene* Blackwall 1833 (Linyphiidae) based on its original description and illustrations.

Keywords: Taxonomy, Oriental region, Eresoidea, Linyphiidae, Taiwan

The spider family Oecobiidae has a worldwide distribution and is represented in several countries both by native and some cosmopolitan and synanthropic species (Santos & Gonzaga 2003; Platnick 2008). Despite its ubiquity, this family is still in need of revision in several biogeographic regions, with a few exceptions like the Americas (Shear 1970; Santos & Gonzaga 2003) and parts of the Afrotropical region (Shear & Benoit 1974; Rheims et al. 2007). Nine species are known in Eastern Asia, although this figure probably underestimates the true species richness given that the fauna of that region is poorly studied. The literature on Asian oecobiids is relatively rich, including some short taxonomic studies that allow the identification of common species in the region (Kim & Lee 1998; Song et al. 1999). However, at least two Asian species of the genus *Oecobius* Lucas 1846 are particularly problematic since the type material of both species is lost. The first of them, *Oecobius formosensis* (Kishida 1943), has been illustrated and recorded twice for Taiwan (Kayashima 1943; Lee 1966) but is insufficiently known mainly due to the scarcity of good illustrations. The second, *Oecobius sapporense* Saito 1934, was described based on a female specimen from northern Japan and is represented in the literature by good illustrations (see Saito 1934), which is interesting since these illustrations clearly and unmistakably suggest that *O. sapporense* is not a member of the family Oecobiidae. This problem was already noticed by some authors (Shear 1970; Yaginuma 1977), but a solution has never been proposed possibly because, as mentioned above, no specimens are available for study. In this note we discuss the situation of these problematic Asian species and propose nomenclatural solutions given the information currently available. Additionally, three worldwide species of *Oecobius* are here recorded for the first time in Taiwan, based on new specimens examined and on published evidence. The material examined for this study is deposited in Instituto Butantan, São Paulo (IBSP, A.D. Brescovit, curator) and National Science Museum, Tokyo (NSMT, H. Ono, curator).

Family Oecobiidae Blackwall 1862

Oecobius formosensis (Kishida 1943)

Phanerecobius formosensis Kishida, in Kayashima 1943:16, pl. 8, fig. 2. *Oecobius formosensis*, Lee 1966:18, figs. 3a–d.

Type material.—TAIWAN: T'ai-nan, K. Kishida coll., one specimen (adult female or juvenile, not specified), deposited in the collector's personal collection, currently lost.

Remarks.—The original description of this species provides no characters for its proper identification. The only illustration available for the type specimen, showing a dorsal habitus, is extremely reduced in size. This figure depicts what is most probably an oecobiid specimen, but the figure is poor in details. Lee (1966) described and illustrated the male, but no justification is presented that assures that it is conspecific with the specimens studied by Kishida (1943). It is not clear whether the specimen he studied came from the type locality, since the collection locality of the male specimen is not specified. Lee (1966), however, states that the species is widely distributed throughout Taiwan. Lee's description was certainly not based on the examination of the type material, since it was never deposited in any institution and is currently considered lost as is most of the material studied by K. Kishida (Ono 2005; H. Ono personal communication). The illustration of the male pedipalp presented by Lee (1966:fig. 3d), although depicted in an unusual ventral-retrolateral view, clearly suggests it is conspecific with *Oecobius marathaus* Tikader 1962. This conclusion is supported by the presence of two diagnostic characters of *O. marathaus* in Lee's (1966) figure: a pointed lobe (OTL1) situated on a basal tegular projection and a sinuous prolateral sclerite on the tegulum (see Santos & Gonzaga 2003:9, figs. 14, 15). It could be reasonable to consider *O. formosensis* as a senior synonym of *O. marathaus*, but two other *Oecobius* species are here recorded from Taiwan (see below). It is possible that Kishida (1943) studied one of these species, since he states that the type specimen was collected in a house in southern Taiwan. These three species (*O. concinnus* Simon 1893, *O. marathaus*, and *O. navus* Blackwall 1859) are synanthropic and cosmopolitan (Platnick 2008) and can be distinguished by the color pattern of the carapace, as shown by Santos & Gonzaga (2003). However this would not be possible in this case due to the extreme reduction of the original illustration. It is possible to assure that the male illustrated by Lee (1966) is *O. marathaus* but there is no evidence that it is conspecific with the specimen originally studied by Kishida, whose illustrations are too small to distinguish details of coloration. In light of these problems, we propose *Oecobius formosensis* as a *nomen dubium*.

Oecobius navus Blackwall 1859

Oecobius navus Blackwall 1859:266 (for additional published records and synonyms, see Platnick 2008).

Material examined.—TAIWAN: T'ai-chung, Tunghai University Campus (24°10′N, 120°35′E), Chou I-Chia coll., 20.IV.2002, 1♂ 1♀ (IBSP 34955); ibid, 10.IV.2002, 6♀ 1 juv. (IBSP 34954).

Oecobius concinnus Simon 1893

Oecobius concinnus Simon 1893:435, pl. 9, fig. 2 (for additional published records and synonyms, see Platnick 2008).

Material examined.—TAIWAN: T'ai-chung, Tunghai University Campus (24°10′N 120°35′E), Chou I-Chia coll., 20.IV.2002, 1♀ (IBSP 34956).

Oecobius marathaus Tikader 1962

Oecobius marathaus Tikader 1962:684–685, fig. 2 (for additional published records and synonyms, see Platnick 2008).

Remarks.—Although we have not seen any specimen of this species from Taiwan, a male was recorded in that country by Lee (1966), who considered it as the male of *Oecobius formosensis* (see discussion above).

Family Linyphiidae Blackwall 1859

Neriene sapporense (Saito 1934) new combination

Oecobius sapporense Saito 1934:271, pl. 12, figs. 1a–b, pl. 14, figs. 33a–b. Saito 1959:34, fig. 7a–d; Kritscher 1966: 293, fig. 16.

Type material.—JAPAN: *Hokkaido*: Sapporo, 13.IX.1930, S. Saito coll., 1♀, deposited in the collector's personal collection, currently lost.

Remarks.—Although this species has been maintained in Oecobiidae since its description, the original illustrations of dorsal and lateral views of the habitus and of the eye region (Saito 1934:figs. 1a–b, 33a) clearly show it is misplaced in this family (see comments in Shear 1970; Yaginuma 1977). The illustration of the epigynum (Saito 1934: fig. 33b; reproduced from the original by Kritscher 1966) includes a pair of lateral atria separated by a median, posteriorly projected septum. As with other spider species described by Saito (1934), the type material is probably lost (H. Ono personal communieation). Thus, the original illustrations and description are currently the only source of information about this species. Judging by body shape, color pattern, and epigynum structure, this species seems similar to *Neriene nigripectoris* (Oi 1960), a linyphiid widely distributed from Russia to Eastern Asia, including Japan (Oi 1960:227, figs. 330–332; Shinkai & Takano 1984: 24; Chikuni 1989: 50). It is reasonable to consider *O. sapporense* as a senior synonym of *N. nigripectoris*, given their similarity and that the type locality of the former is well within the distribution range of the latter. However, since the type specimen of *O. sapporense* is relatively small (although within the range of variation of *N. nigripectoris*) and has a pair of dark lateral bands on the carapace (which is not known for *N. nigripectoris*), we prefer to keep it as valid a species. The real identity of *N. sapporense* could be determined with future collections from the type locality.

Material examined.—*Neriene nigripectoris* (Oi 1960): JAPAN: *Miyagi-ken*: Sendai-Shi (38°15′N, 140°53′E), Dainohara Shinrin-Koen, 12.VIII.1981, K. Sasabi coll., H. Ono det., 2♂ 3♀ (NSMT-Ar. 503).

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SHORT COMMUNICATION

Males of *Gambaquezonia itimana* (Araneae, Salticidae), with notes on females

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Abstract. Fourteen specimens of the jumping spider *Gambaquezonia itimana* Barrion & Litsinger 1995 were collected in the vicinity of Mt. Makiling and Los Banos, Luzon Island, Philippines. The species was described only from the holotype female. Males are described for the first time, and additional females are documented.

Keywords: Description, new records, Philippines, jumping spider

Barrion & Litsinger (1995) described in some detail *Gambaquezonia itimana* from the female holotype, the only specimen known to them at the time. Murphy and Murphy (2000) redescribed the general appearance. The holotype female was collected in the Philippines on Luzon Island, Quezon Province. Several morphological features of this specimen are unusual, including a large number of ventral macrosetae on legs I and II, prominent sparse rows of elongate setae on the dorsum, a multi-cusped retromarginal tooth, and an epigynum which superficially looks like an euophryine, but structurally is quite different. Knowledge of the male may help clarify the relationships of this species.

Multiple research visits to the Philippines were made by Robert R. Jackson from 1993 to 2000. I accompanied Simon Pollard and him on a salticid survey for three weeks in 1993. In 2002, I undertook to identify the many Philippine salticids collected by Jackson and colleagues, myself included. This is the first of several planned papers that will document taxonomic changes or additions to the Philippine salticid fauna as a result of those collections. Surveys from Luzon Island, Laguna Province, Los Banos (and nearby Mt. Makiling) found 3 males, 8 females, and 3 subadult females of *G. itimana*. Males are described for the first time. The additional females are documented and morphological variation is recorded.

The abbreviations BL = body length [excluding anterior median eyes, anal tubercle, spinnerets, and pedicel (if visible)], CL = carapace length, CW = carapace width, PLV = prolateroventral (followed by number of macrosetae), RLV = retrolateroventral (as in PLV), and RTA = retrolateral tibial apophysis are used in the descriptions. Range of measurements (in mm) is indicated in the format: min (mean) max. Literature citations follow Platnick (2008). Digital photographic figures were made with an Automontage system (Syncroscopy, Cambridge, UK).

Gambaquezonia Barrion & Litsinger 1995

Diagnosis.—The genus is monotypic and defined by the following combination of characters: Dual longitudinal rows of graduated elongate setae on the dorsum of carapace and abdomen; 5 or more macrosetae on venter of tibia I and metatarsus I on each of the prolateral and retrolateral edges; cheliceral promargin with two teeth (fused basally in male), retromarginal tooth with 4–5 cusps (possibly multiple teeth fused basally); male chelicerae excavate medially with spine at top of excavation; color pattern distinctive, with X-shaped anterior abdominal striping, and two pairs posterior abdominal spots of which the more anterior pair may be fused into a transverse band; anal tubercle pigmented with posterior pointed tip; embolus a retrolateral spiral from a disc; epigynal openings medial, set in oval depressions below atrial rims (not all on same plane as in many euophryines).

Gambaquezonia itimana Barrion & Litsinger 1995

Figs. 1–13

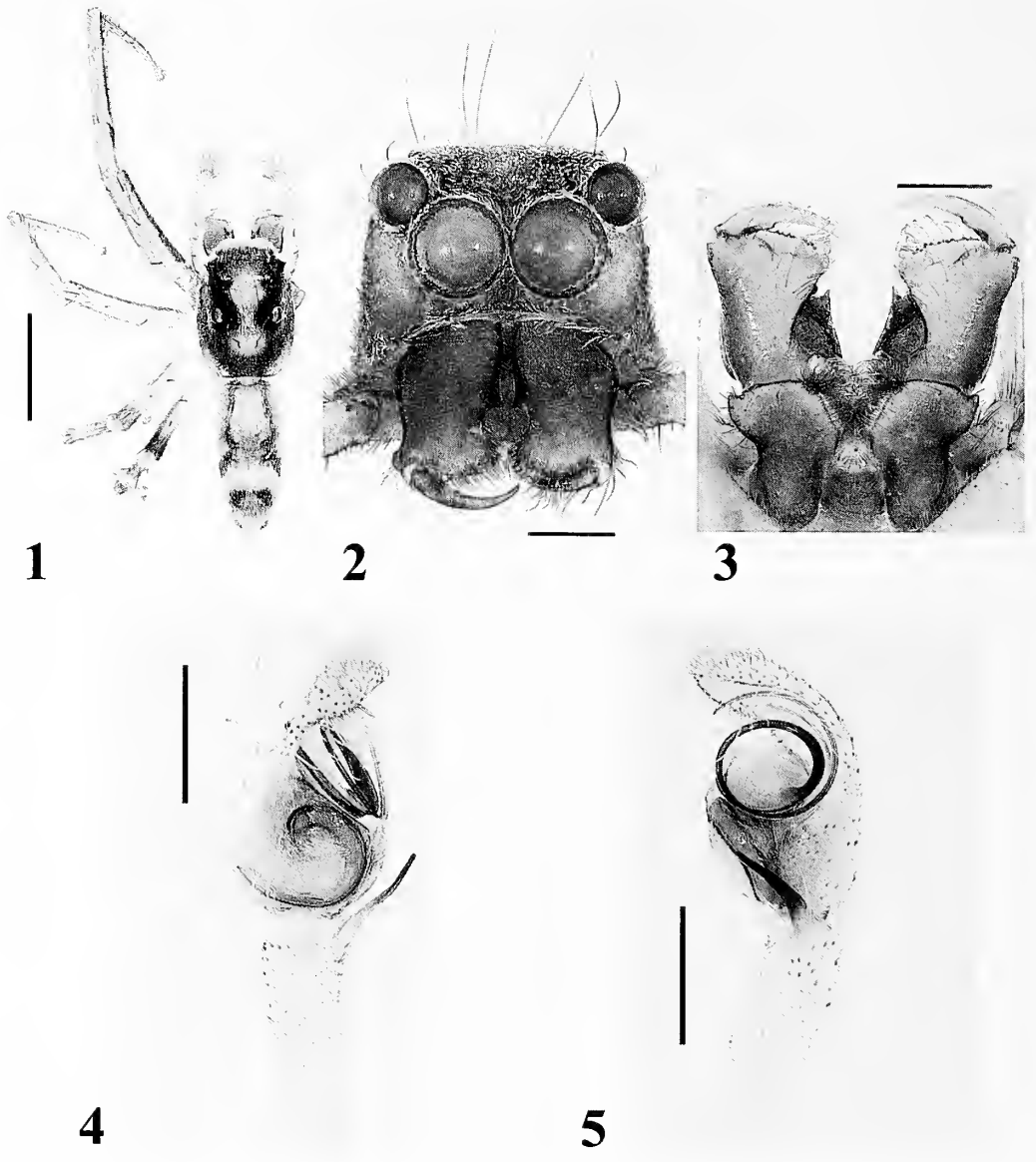
G. i. Barrion & Litsinger 1995:95, f. 49°–e (Df).

Type data.—Philippines: Luzon Island: Quezon Province, Real, Llavac village [14°39′N, 121°36′E], 26 August 1985, holotype female (M. Perez, IRRI).

Material examined.—Philippines: Luzon Island: *Laguna Province*: Los Banos, IRRI station [14°10′N, 121°13′E]: Feb 1993, 1m (R.R. Jackson, Ph237/93); Jan 1994, 1f (R.R. Jackson, Ph1733/93); Dec 1996, 1f (R.R. Jackson, Ph219/96); Jan 1997, 1f (R.R. Jackson, Ph884/96); Mt. Makiling Forest Reserve [14°08′N, 121°11′E]: Mar 1993, 1f (R.R. Jackson, Ph388/93); 30 Nov–17 Dec 1993, 1m 1f 1juv (G.B. Edwards); Dec 1993, 1 juv (R.R. Jackson, Ph1240/93); Dec 1996, 1f (R.R. Jackson, Ph256/96); Jan 1997, 2f (R.R. Jackson, Ph532/96); Jan 1997, 1m (R.R. Jackson, Ph716/96); Jan 1997, 1 juv (R.R. Jackson, Ph742/96). All specimens (except the holotype) are deposited at the FSCA.

Description.—This medium-sized, rather delicate salticid is unusual in having a wide multi-cusped (4–5 cusps) retromarginal cheliceral tooth (Figs. 3, 12), an unusually large number of leg macrosetae (Fig. 13), and two sparse paramedial rows of graduated elongate setae that look like an antennal array on the dorsum of the body, especially on the carapace (Fig. 8), with a few similar setae also occurring on the legs dorsally. The setal arrangement suggests that this species might have interesting and unusual behavior or sensitivity to an as yet unknown stimulus. For example, the graduated array of dorsal setae may be attuned to a set of airborne vibrations which might be used in a sexual context, either by detecting sound or by detecting pheromone emissions, similar to moth antennae. Alternatively, these setae may similarly be used in prey detection, which, along with the unusual leg macrosetae and cheliceral teeth, might indicate a specialization for a particular prey type.

Females (n = 8): CL = 2.16 (2.32) 2.41, CW = 1.54 (1.66) 1.73, BL = 4.94 (5.64) 6.30. Females vary in the amount of pigmentation of the dorsal markings (Figs. 6, 7 show extremes) and as indicated below. Interestingly, the anal tubercle is darkly pigmented (and has a pointed tip); however, the spinnerets lack this pigmentation. The ventral leg macrosetae do not strictly occur in pairs and are better described as a row of prolateroventral and a row of retrolateroventral macrosetae. From zero to three are considerably smaller than the others in a row. All femora have 3 dorsal macrosetae in a longitudinal row (typical for salticids), with a dorsoprolateral macroseta and a dorsoretrolateral macroseta near the most distal of the dorsal macrosetae. Also, femur II has a retrolateral macroseta in the middle of the segment, and femur III has a prolateral macroseta in the middle of the segment. These are uncommon placements for femoral macrosetae in salticids. Other total leg I macrosetae numbers: tibiae PLV row 5–7, RLV row 5–10, plus 1 prolateral about ¼ to 1/3 length

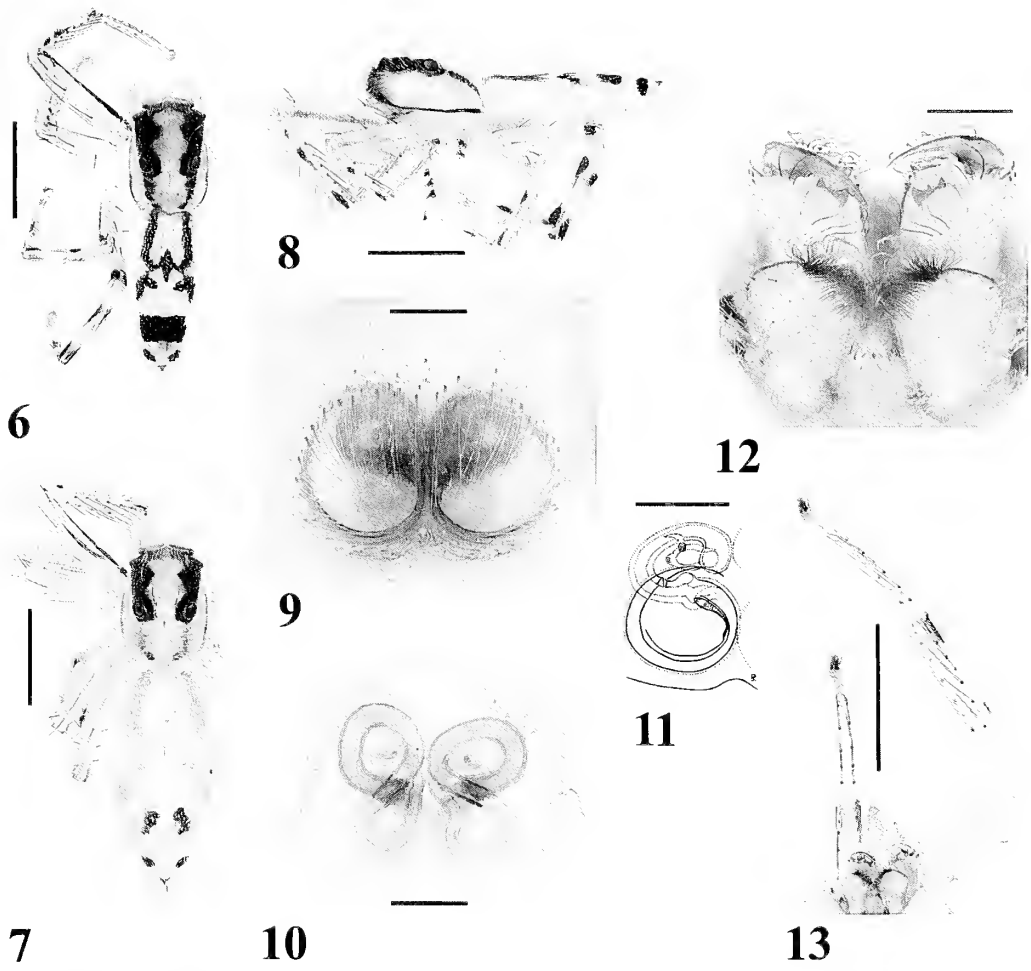


Figures 1–5.—*Gambaquezonia itimana* Barrion & Litsinger, male. 1. Dorsal habitus; 2. Face; 3. Chelicerae ventral view; 4. Left palp ventral view; 5. Left palp retrolateral view. Scale line for Fig. 1 = 2 mm; scale lines for Figs. 2, 3, 4, 5 = 0.5 mm.

from distal end; metatarsi PLV row 6–8, RLV row 6–7, plus 1 distal retrolateral and/or 1 proximal retrolateral (or both absent). Often the macrosetae numbers on the legs are asymmetrical. The lighter, more central parts of the epigynum (Figs. 9–11) are depressed below the sclerotized atrial rims. The copulatory openings are placed at mid-length, next to the septum formed by the rims.

Males (n = 3): CL = 2.35 (2.40) 2.47, CW = 1.73 (1.77) 1.85, BL = 5.31 (5.48) 5.62. Males (Fig. 1) are essentially like females in appearance, except there is a broad dark band on the back and sides of the carapace, abdominal markings are more obscure, and the dorsum is more noticeably covered in iridescent scales (some females also have dorsal iridescent scales). The chelicerae (Fig. 2) are excavate medially, with an integumental projection (essentially a true spine, neither a tooth nor a typical mastidion) at the top of the excavation. The endites each have an anterolateral cusp. Femoral macrosetae are like the female. Other leg I macrosetae: tibiae PLV row 5–7, RLV row 5–8, plus 1 prolateral about ¼ to 1/3 length from distal end; metatarsi PLV row 6–8, RLV row 5–8, plus 1 proximal retrolateral (prolateral in one specimen). The palp (Figs. 4, 5) has a RTA that is elongate, flattened, slightly curved, blunt tipped, and angled toward the venter. The embolus faces retrolaterally, and during mating seems like it would fit underneath (from a ventral position) an atrial rim, which would act as a guide to the copulatory opening. The embolus has a basal embolar disc reminiscent of a euophryine, but the bulb sperm duct lacks the S-shaped extra bend characteristic of that subfamily. The embolus is otherwise similar to several genera in the Ballinae, but the other characters used to diagnose that subfamily (Benjamin 2004) do not fit *G. itimana*. It seems likely that the closest relative will be found among those salticids related to the Astieae, the main salticoid group in the region with relatives retaining the plesiomorphic condition of pluridentate retromarginal cheliceral teeth, from whence the multi-cusped retromarginal tooth of *G. itimana* might be derived.

My thanks to Robert R. Jackson for his support and encouragement, for our longterm friendship and collaboration (which, among other things, has greatly aided the accumulation of a fantastic collection of tropical salticids), and for his outstanding research on the jumping spiders. I would also like to thank Alberto T. Barrion for his hospitality at the International Rice Research Institute (IRRI) during my visit to the Philippines, and Jerzy Proszynski, who kindly provided the drawing (Fig. 11) of the epigynum of the type. This is FDACS/DPI, Entomology Section contribution #1091.



Figures 6–13.—*Gambaquezonia itimana* Barrion & Litsinger, female. 6. Heavily pigmented dorsal habitus; 7. Lightly pigmented dorsal gravid habitus; 8. Habitus lateral view; 9. Epigynum ventral view; 10. Epigynum dorsal view cleared; 11. Holotype epigynum ventral view cleared; 12. Chelicerae ventral view; 13, Left leg I retrolateroventral view, also showing distal end of right leg I ventral view. Scale lines for Figs. 6, 7, 8, 13 = 2 mm; scale lines for Figs. 9, 10, 11 = 0.25 mm; scale line for Fig. 12 = 0.5 mm.

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SHORT COMMUNICATION

Widespread infections by the bacterial endosymbiont *Cardinium* in arachnids

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Abstract. Maternally inherited bacterial endosymbionts such as *Wolbachia* can potentially have a major impact on the reproduction of their arthropod hosts. Most previous studies have focused on the effects on insects, but recent evidence demonstrates that the endosymbionts *Wolbachia*, *Rickettsia*, and *Spiroplasma* are also common in spiders. Such infections potentially explain observed characteristics of reproduction in this group such as skewed sex ratios or reported cases of parthenogenesis. Here we test spiders and a range of other arachnids for infection with another, more recently described maternally acquired endosymbiont, *Cardinium*. We present data from a survey of spiders and other arachnids collected in the field and obtained from museum collections. Infections with *Cardinium* are found to be very widespread, perhaps more so than in other arthropod groups. The consequences of this and directions for future research on endosymbiont-arachnid interactions are discussed.

Keywords: *Rickettsia*, *Spiroplasma*, *Wolbachia*, spider, cytoplasmic incompatibility

Maternally inherited endosymbionts such as *Wolbachia*, *Rickettsia*, and *Spiroplasma* species are known to affect reproductive and behavioral traits of their predominantly arthropod hosts (see Charlat et al. 2003). Such infections are relatively widespread in insects and mites and recent evidence indicates that they are also found in both haplogyne and entelegyne spiders (Oh et al. 2000; Cordaux et al. 2001; Rowley et al. 2004; Goodacre et al. 2006). Incidences of multiple infections were also found to be common (Goodacre et al. 2006).

Table 1.—Examples of potential hallmarks of endosymbiont infection in arachnid species;* denotes where the same species was tested by PCR and found to harbor *Cardinium* (Table 2).

Hallmark	Family	Species
Acarina		
Parthenogenesis	Argasidae	*Ornithodorus spp.*
Parthenogenesis	Ixodidae	*Amblyomma agamum* Aragão 1912, *Amblyomma dissimile* Koch 1844*, *Boophilus microplus* Canestrini 1887, *Haemaphysalis bispinosa* Neumann 1897, *Hyalomma* spp, *Rhipicephalus bursa* Canestrini and Fanzago 1877.
Parthenogenesis	Trombiculidae	*Leptotrombidium arenicola* Traub, 1960
Scorpiones		
Parthenogenesis	Buthidae	*Ananteris coinaui* Lourenço 1982, *Hottentota hottentota* Fabricius 1787, *Tityus columbianus* Thorell 1876, *Tityus metuendus* Pocock 1897, *Tityus stigmurus* Thorell 1876, *Tityus trivittatus* Kraepelin 1898, *Tityus uruguayensis* Borelli, 1901
Parthenogenesis	Hemiscorpiidae	*Liocheles australasiae* Fabricius, 1775*
Opiliones		
Parthenogenesis	Caddidae	*Acropsopilio chomulae* Goodnight & Goodnight 1948
Parthenogenesis	Phalangiidae	*Leiobunum globosum* Suzuki 1953, *Leiobunum manubriatum* Karsch 1881
Araneae		
Absence of males or strongly biased sex-ratio	Symphytognathidae	*Anapistula caecula* Baert & Jocqué 1993
Absence of males or strongly biased sex-ratio	Araneidae	*Hypognatha* spp.
Reduced viability of offspring from inter-population crosses	Salticidae	*Habronattus pugillus* Griswold 1987
Primary SR distortion	Linyphiidae	*Pityohyphantes phrygianus* Koch 1836
Primary SR distortion	Eresidae	*Stegodyphus dumicola* Pocock 1898
Primary SR distortion	Theridiidae	*Anelosimus domingo* Levi 1963
Primary SR distortion	Thomisidae	*Diaea socialis* Main 1988
Parthenogenesis	Dysderidae	*Dysdera hungarica* Kulczyn'ski 1897
Parthenogenesis	Ochyroceratidae	*Theotima minutissima* Petrunkevitch 1929
Parthenogenesis (suggested)	Amaurobiidae	*Coelotes* spp.

Table 2.—Overview of results of PCR screens for *Cardinium* in various arachnid species. Key to symbols: *[1]Sources - abbreviations: FM: Field Museum Chicago; GS: Gioia Schwarzenbach, University of Zurich, mites collected from Fehraltorf, Switzerland; MV: collection by Marija Vugdelic, unknown thomisid collected in the Balkans; OM: collected by O. Y. Martin in Norwich, United Kingdom; *[2] i.e. specimens tested; f = females, m = males, j = juveniles, e = egg sacs, of unknown sex if not specified; *[3] i.e. specimens found to harbor *Cardinium*; *[4] 1 = a DNA preparation of 3 individuals of unknown sex, *[5]parthenogenetic.

	Genus	Species		*[1]	Number tested*[2]	Number of positives*[3]
Acarina						
Ixodidae	*Amblyomma*	*cajennense*	Fabricius 1787	FM	3	2
Ixodidae	*Amblyomma*	*dissimile*	Koch 1844	FM	2f 1m	1f 1m
Nothridae	*Nothrus*	*sp.*		FM	1*[4]	1
Siteroptidae	*Pediculoides*	*mesembrinae*	Canestrini 1880	GS	2	2
Scorpiones						
Liochelidae	*Liocheles*	*australasiae*	Fabricius 1775	FM	2f*[5]	2f
Opiliones						
Phalangidae	*Phalangium*	*opilio*	Linnaeus 1761	FM	3f	3f
Phalangidae	unknown			OM	1f	1f
Araneae						
Agelenidae	*Tegenaria*	*duellica*	Simon 1875	OM	1f 1m 2j	1f 1m 2j
Araneidae	*Araneus*	*diadematus*	Clerck 1757	OM	4f1m	2f
	Zygiella	*x-notata*	Clerck 1757	OM	4f	4f
Linyphiidae	*Lepthyphantes*	*minutus*	Blackwall 1833	OM	1	1
Liocranidae	unknown			OM	1f	1f
Pholcidae	*Pholcus*	*phalangioides*	Fuesslin 1775	OM	1m	1m
Salticidae	*Ghelna*	*canadensis*	Banks 1897	FM	2f 1m	2f 1m
	Habrocestum	*pulex*	Walckenaer 1837	FM	1f 1m	1f 1m
	Maevia	*inclemens*	Koch 1846	FM	2f 1m	2f
	Marpissa	*lineata*	Hentz 1846	FM	2f	1f
	Neon	*neli*	Peckham & Peckham 1888	FM	2f	2f
	Pelegrina	*proterva*	Walckenaer 1837	FM	1f 1m	1f
	Phidippus	*audax*	Hentz 1845	FM	1f	1f
	Salticus	*scenicus*	Clerck 1757	OM	3f	3f
Tetragnathidae	*Meta*	*mengei*	Blackwall 1870	OM	4f 2m 1e	2f 2m
	Tetragnatha	*montana*	Simon 1874	OM	3j	2
Theridiidae	*Enoplognatha*	*ovata*	Clerck 1757	OM	1f 1m	1f 1m
Thomisidae	unknown			MV	1	1

Another endosymbiont, *Cardinium*, has been described more recently (Zchori-Fein et al. 2004). *Cardinium* is known to infect nematodes (Noel & Atibalentja 2006), insects (Provencher et al. 2005; Bigliardi et al. 2006; Marzorati et al. 2006) and mites (Chigira & Miura 2005; Groot & Breeuwer 2006). A recent study shows that it is also found in spiders (Duron et al. 2008), although its occurrence in other groups of arachnids has not yet been established.

The effects of endosymbionts such as *Wolbachia* or *Cardinium* on their hosts can include skewing the sex ratio (SR) towards females (due to an increased male mortality rate, a feminization of males, or a resulting parthenogenesis) or cytoplasmic incompatibility (Engelstädter et al. 2006) where uninfected individuals are at a reproductive disadvantage. The consequence of such infection has been studied in mites, but little research has focused on the arachnids as a whole despite the fact that various species or population traits such as distorted SR, parthenogenesis, and potential CI could potentially be explained by the presence of such microbes (see Table 1 for a summary of examples compiled from the literature; references supplied on request; see also Goodacre et al. 2006). These phenomena may have other well-founded explanations, but the possibility that they are the consequence of endosymbiont infections cannot be evaluated without testing for infections in such "hallmark" species.

Various arachnids (Acari, Opiliones, Scorpiones, and Araneae) were assembled for this survey and assessed for infection with *Cardinium*. A major portion of the species included were borrowed from the collection of the Field Museum Chicago, including species known to exhibit potential hallmarks of infection (see Table 1) or closely related species. These samples were supplemented with an additional subset of arachnid samples from the authors' collections held at the University of East Anglia. DNA was extracted from a combined sample comprising both leg and abdominal tissue for females and leg and palp (where possible) for males. DNA was extracted using QIAGEN DNEasy® kits and eluted in 100 µl distilled water (see Goodacre et al. 2006 for further information). The localization of *Cardinium* in particular hosts is not yet established and it may not be equally distributed through all host tissue types. However, it is always likely to be closely-associated with reproductive tissue given its vertical method of transmission. DNA was therefore extracted from tissue that included reproductive organs (ovary containing abdominal tissue and male palps respectively) in order to maximize the chances of detecting any bacteria present, while avoiding areas such as the mouthparts, which are potentially contaminated with non-spider tissue. All samples were tested for *Cardinium* using PCR methods described by Zchori-Fein & Perlman (2004), which involves amplifying a section of the *Cardinium* 16S rRNA gene and visualizing the amplified DNA using gel electrophoresis. A summary of the specimens tested and the results of the PCR tests are given in Table 2.

Our study shows that *Cardinium* is present in a range of diverse arachnid groups and appears to be much more common than in the insects that had been assessed previously (Table 2). The infection was found in at least 1 representative of all of the species tested (100% infected, $n = 25$) vs. 6% of insect species in Zchori-Fein & Perlman 2004 (of which 24% harbored *Wolbachia*). This finding echoes that of

another recent study of spiders, which also found *Cardinium* to be more common than in insects (22% of spider species infected, Duron et al. 2008). Furthermore, *Cardinium* seems to be more common in spiders than are the other three endosymbionts that have been isolated in this group of hosts (Goodacre et al. 2006). The small sample sizes in our study do not allow us to test for differences in infection between the sexes in individual species. We note, however, that there was no significant difference overall between the males and females in their likelihood of carrying the infection (84% females (n = 37) and 73% males (n = 11) infected, Exact Test P = 0.49).

Further research will pinpoint more precisely how widespread this microbe is within and among arachnid groups and will allow us to understand the effects on individual arachnid hosts. Future work will be directed towards identifying the phenotypes caused by individual bacteria, and in determining the selective advantage that the phenotype confers, and studying the consequence of co-infection with more than one endosymbiont. Spiders are a particularly well-suited group (see Goodacre et al. 2006) for testing theoretical predictions regarding evolutionary relationships between endosymbiont infection and host traits, particularly reproductive traits under sexual selection. Endosymbionts such as *Cardinium* can specifically impact such traits, being potentially involved in both interspecific conflict between host and symbiont, as well as intraspecific sexual conflict between the sexes (see Martin & Gage 2007). A powerful means of illuminating the separate and combined action of these evolutionary conflicts would be to apply an artificial selection approach similar to previous experiments focusing on sexual conflict (e.g., Martin & Hosken 2003).

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SHORT COMMUNICATION

Prey capture by the whip spider *Phrynus marginemaculatus* C.L. Koch

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Abstract. Whip spiders (Arachnida, Amblypygi) are little-studied arachnids with enlarged spiny pedipalps and elongated "antenniform" forelegs. These antenniform legs contain at least seven giant sensory neurons with no known behavioral function. Here we use high-speed einematography to describe the prey capture behavior of the whip spider *Phrynus marginemaculatus* C.L. Koch 1840, in order to examine how these giant neurons might be involved. When presented with a prey item (a cricket), a whip spider first accurately aims one of its antenniform legs in the prey's direction. Next, the whip spider orients its body to the prey item and approaches, placing one antenniform leg tip on either side of the prey. The whip spider may remain relatively still in this position for some time, before opening its pedipalps in preparation for a strike and then rapidly swinging its antenniform legs away from the prey item and striking at it with its pedipalps. In common with previous studies, our results show that giant neuron activity is not necessary to trigger any of the stages of normal prey capture behavior, but they also suggest that these neurons could still provide information important in this context.

Keywords: High-speed film, predator, attack

Whip spiders (Arachnida, Amblypygi) possess a number of morphological specializations including enlarged spiny pedipalps and elongated antenniform forelegs which they use as feelers. These antenniform legs are equipped with a variety of sensory organs (Igelmund 1987; Weygoldt 2000), and mechanosensory information from some of these organs is rapidly transmitted to the central nervous system by at least seven identified giant neurons (GNs) (Igelmund & Wendler 1991a). The response properties of four of these neurons are now known: interneurons GN1 and 2 are mechanosensory and respond to mechanical contacts with the bristle hairs on the antenniform leg tarsus; sensory neurons GN6 and 7 are proprioceptors that detect bending of the tarsus around a particular joint (Igelmund & Wendler 1991a, b). The behavioral function of these giant neurons is unknown, but their presence in whip spiders from very different habitats indicates that they may play a role in fundamental behavior (Spence & Hebets 2007); one suggestion has been that they function in prey capture (see Weygoldt 2000).

The antenniform legs, and their GNs, are not necessary for successful prey capture since a whip spider that has autotomized both of these limbs can still capture prey (Beck & Görke 1974; Weygoldt 1995, 2000). In contrast, removal of the trichobothria – air movement-sensitive hairs predominantly located on the walking legs – leaves a whip spider unable to orient towards or capture moving prey (Beck & Görke 1974; Weygoldt 1995, 2000), demonstrating that these hairs are necessary and sufficient for successful prey capture. Nevertheless, this evidence does not preclude a secondary role for the GNs in prey capture when they are intact, and field observations suggest that they might play a role in the capture of aquatic prey during the fishing behavior of the whip spider *Heterophrynus cheiracanthus* Gervais 1842 (Ladle & Velander 2003). In this note we use high-speed cinematography to examine the possible role of the GNs in the capture of terrestrial prey and to provide a detailed kinematic description of this behavior.

We collected *Phrynus marginemaculatus* C.L. Koch 1840 from the Pine Rock hammock on Big Pine Key, FL, USA (24°42′33.49″N, 81°22′56.73″W), and housed them in our laboratory under a 12:12 h light-dark cycle. Voucher specimens have been deposited in the collection of the University of Nebraska State Museum (accession number: 272; specimen numbers: 3257774, 3257775). We performed experiments on six adult female whip spiders since we used the males we collected in an unrelated study (Santer & Hebets 2008). However, informal observations of the feeding behavior of these males revealed no differences from that of females. In order to allow prey capture behavior to be filmed, we permanently housed whip spiders in cages (10 cm × 10 cm × 11 cm) custom built from sheets of clear acetate. Aluminum screening was placed on the rear wall of all cages, providing a surface upon which the animals could climb. Whip spiders would remain on the screening, allowing a prey item to be introduced and prey capture behavior to be filmed, without transferring the whip spider to an experimental arena. We introduced a prey item once every two weeks during the light phase of the light cycle and filmed the resulting predator-prey interaction at 60 or 250 fps from two angles (cage front and side) using a Photron Fastcam 1024 PCI camera and mirror.

When collecting *P. marginemaculatus* we commonly found them alongside numerous cockroaches, small scorpions, and centipedes. We therefore believe that ground dwelling invertebrates form the bulk of *P. marginemaculatus*' diet. In the laboratory, two-week old crickets were readily attacked and eaten and so we use them as a typical prey item in this study. Little data are available on the natural diet of whip spiders, but their main food is thought to consist principally of arthropods, particularly insects (Weygoldt 2000). Crickets and cockroaches are a known part of the diet of a related whip spider species, *Phrynus pseudoparvulus* Armas & Víquez 2001 (previously thought to be *Phrynus parvulus*, Armas & Víquez 2001), for which feeding data are available (Hebets 2002). *Phrynus pseudoparvulus* has also been observed feeding on moths captured in flight (Hebets 2002), but when we presented *P. marginemaculatus* with moths collected locally in Lincoln, NE, USA, we found that moths were rarely attacked and that the whip spiders were often startled by a moth's flapping movements. This may indicate that moths are not a typical part of *P. marginemaculatus*' diet or that the species presented were inappropriate.

In total, we successfully filmed 27 high-speed video sequences in which a whip spider attacked a cricket by striking at it with its pedipalps (minimum of one prey capture per whip spider). Across these sequences, prey capture behaviors were remarkably similar and preparatory behaviors comprised a sequence of three distinct behavioral actions:

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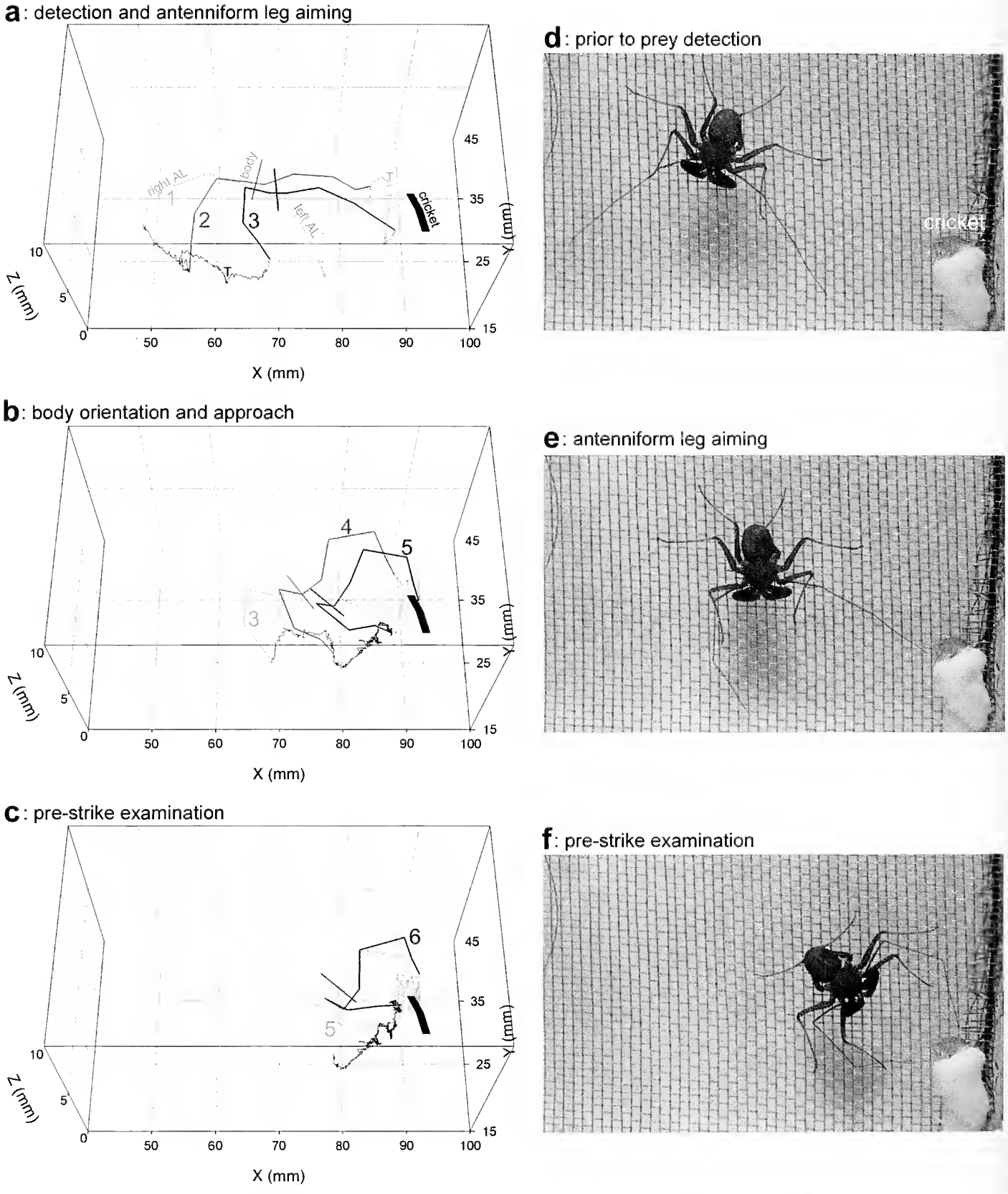

Figure 1.—The typical sequence of preparatory behaviors preceding a prey capture strike in *Phrynus marginemaculatus*. Panels **a**–**c** describe the three principal behavioral phases transcribed from each frame of a typical prey capture sequence recorded at 60 fps. In each panel, the whip spider's body and antenniform leg positions are plotted at intervals as solid lines (labeled "left AL," "body," "right AL" in panel **a**). The grayscale of these lines and the associated number indicates their position in the sequence (1 = 0 ms, 2 = 2000 ms, 3 = 5500 ms, 4 = 7167 ms, 5 = 15500 ms, 6 = 23333 ms). In addition, left and right antenniform leg tip positions are plotted at each frame (light gray and black jagged traces

(1) Prey detection and antenniform leg aiming.—After a cricket was released into its cage, the first notable action by the whip spider was to aim one or other of its antenniform legs in the direction of the prey item without re-orientation of its body (Figs. 1a, e). This action occurred in 88.9% of filmed feeding events (the remainder resulting from the cricket actually walking into the whip spider apparently before detection). Since the walking leg trichobothria are necessary and sufficient for successful prey capture (Beck & Görke 1974; Weygoldt 1995), it seems likely that they could also be responsible for initial prey detection. The trichobothria could provide the necessary directional information for antenniform leg aiming (e.g., Friedel & Barth 1997). Antenniform leg aiming could last indefinitely in trials where the cricket was not ultimately attacked, or until the next phase of the prey capture sequence occurred when it was.

(2) Body orientation and approach.—Following a period of antenniform leg aiming, whip spiders re-oriented their bodies towards the cricket or slowly approached it until it was within the tips of the antenniform legs and normally until the long axis of their body was in line with the cricket (Fig. 1b). During this phase, the antenniform leg tips sometimes (in 55.6% of trials) made repeated gentle contacts with the cricket that may have been attempts at chemical examination; these contacts did not startle the cricket. In cases where the cricket walked into the antenniform leg, the antenniform leg was withdrawn rapidly (see also Foelix & Troyer 1980). Body orientation and approach occurred in 85.2% of the filmed feeding trials.

(3) Pre-strike prey examination.—The final preparatory action before a strike was for the whip spider to place its left and right antenniform legs on either side of the prey item, usually without making contact with it (Figs. 1c, f). This behavior may be an attempt to examine the odor of the prey item (Hebets & Chapman 2000). Such behavior occurred in 77.8% of trials, although in the remainder of trials examination by one antenniform leg only often occurred. During prey examination, the left antenniform leg tip was placed 2.97 ± 0.59 mm from the nearest part of the cricket's body or appendage (range: 0.00–9.00 mm), and the right antenniform leg 3.13 ± 0.65 mm from it (range: 0.00–12.87 mm) (n = 27 in both cases; measurements made immediately prior to a prey capture strike; here and throughout means ± SEM). From the 27 filmed prey capture sequences, eight could have included fleeting contact between the whip spider's antenniform leg and the limbs, antennae, or cerci of the cricket during pre-strike examination. Whether contact occurred in these trials could not be firmly established from the recorded videos. In the 21 trials where examination of the prey item using both antenniform legs occurred, it had a mean duration of 3.74 ± 1.15 s (range: 0.04–21.33 s) (n = 21).

Following these preparatory behaviors, a whip spider struck at its prey using its pedipalps. The prey capture strike was remarkably stereotyped between trials. Following pre-strike prey examination, the pedipalps were slowly opened, the chelicerae extended, and the whip spider rapidly rocked forwards on its six walking legs. Normally these legs maintained contact with the screened cage wall (where the whip spider usually stood), but sometimes it "jumped." During this strike, the antenniform legs were rapidly swung outwards and rearwards from their pre-strike examination positions, presumably to ensure that they were not damaged by the strike. Strikes were initiated with the prey item at a mean distance of 14.03 ± 0.70 mm from the chelicerae (range: 6.77–20.21 mm) (n = 27). Strikes covered this distance with a mean speed of 0.17 ± 0.02 ms^{-1} (range: 0.008–0.326 ms^{-1}). However, often the strike itself would consist of two phases: an initially slow approach lunge phase followed by an extremely fast one. Mean maximum acceleration (measured frame by frame from each recording) was 18.74 ± 3.12 ms^{-2} (range: 3.09–59.37 ms^{-2}).

Our high-speed video sequences revealed no reliable associations between mechanical contacts that might excite the GNs and the typical stages of prey capture behavior. For example, the antenniform leg tips are held very close to a potential prey item during pre-strike examination but because physical contact is unusual, the mechanosensory neurons GN1, 2, 6 and 7 cannot be necessary to trigger a prey capture strike (see also Foelix & Hebets 2001). Thus GN activity cannot be responsible for triggering the typical sequence of prey capture behaviors, as indicated by previous studies (Beck & Görke 1974; Weygoldt 1995, 2000). Nevertheless, our results do suggest that the GNs have an important role to play in supplying sensory information for prey capture behavior.

Firstly, the antenniform legs sometimes repeatedly contacted the cricket during body orientation and approach, but did not startle it. A fast conducting mechanoreceptive neuron like GN1 would be needed to ensure that these contacts were sufficiently gentle.

Secondly, since the antenniform leg tips are placed on either side of the prey item during pre-strike examination, any movement of the prey item would contact the antenniform leg and excite GN1 or 2. Although this activity is not necessary for prey capture, we did see instances where it could have alerted the whip spider to a sudden and unpredicted prey movement and where it was immediately followed by a strike.

Finally, in one video sequence we noted that the whip spider lost the position of its prey item during antenniform leg aiming. The cricket then approached the whip spider apparently undetected from behind and made contact with one of its antenniform legs. This triggered a rapid re-orientation by the whip spider followed by a sequence of pre-strike examination. The re-orientation began less than 16.6 ms (one frame) after contact by the cricket and contact occurred with the area of the antenniform leg tarsus from which GN2 receives excitation. From here, impulses have approximately 28 mm to travel to the central nervous system and, using a conduction velocity of 2.6 ms^{-1} for GN2 (Spence & Hebets 2007), they could cover this distance in 10.8 ms. Thus this re-orientation is likely to have been GN2-mediated since neurons of smaller diameter could not convey impulses sufficiently rapidly. On several occasions the antenniform leg was rapidly withdrawn if the cricket contacted it, and these movements may also have been GN-mediated (see also Foelix & Troyer 1980). If the function of the GNs were highly context dependent, this could explain why motor responses were not previously found to be reliably associated with GN activity (Igelmund & Wendler 1991b).

In this note we have described the prey capture behavior of the whip spider *P. marginemaculatus*. We confirmed that the GNs were

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labeled "T" in panel **a**). In this sequence the whip spider is preparing to attack a cricket. The cricket's position is plotted as a thick black line (marked "crieket" in panel **a**). Panels **d–f** are example frames from the high-speed video sequence from which panels **a–c** were transcribed. In each frame the cricket sits on a moistened cotton wick in the bottom right corner of the frame ("cricket" in panel **d**). Typically, when a prey item is detected, a whip spider aims its antenniform leg at it without reorienting its body (0–5500 ms; **a**). The whip spider's antenniform leg positions before and during antenniform leg aiming are illustrated in frames **d** and **e**. Following antenniform leg aiming, the whip spider re-orients and approaches the prey item, placing one antenniform leg tip on either side of it (5500–15500 ms; **b**). The whip spider remains relatively still with its antenniform leg tips either side of the prey item, but not usually contacting it, during a phase of pre-strike examination (15500–23333 ms; **c**). Typical antenniform leg positions at the onset of pre-strike examination are illustrated in frame **f**. Following pre-strike examination, a prey capture strike is initiated (see text).

not necessary for triggering any of the typieal stages of prey capture, but our data did indicate several supporting roles that the GNs might play in this eontext. Future study will be necessary to understand these roles and why GNs have evolved in whip spiders.

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SHORT COMMUNICATION

Feeding behavior of trunk-living jumping spiders (Salticidae) in a coastal primary forest in The Gambia

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Abstract. We provide a brief report on the feeding behavior of two salticid species in Bijilo Forest, The Gambia: *Holcolaetis vellerea* Simon 1909 and *Menemerus bivittatus* (Dufour 1831). The former was observed consuming a giant huntsman spider ?*Heteropoda* sp. (Sparassidae), which was much larger than itself and represents the first published evidence of araneophagy in this genus. *M. bivittatus* was frequently observed loitering close to, and orientated towards the nest entrance of stingless bees (Apidae, Apinae, Meliponini), watching them as they entered and left, but no other salticid species were observed doing this. Araneophagy and prey-specific predation behavior are well known in salticids but the behaviors reported here have not previously been documented.

Keywords: Araneophagy, *Holcolaetis vellerea*, *Hypotrigona*, *Meliponula*, *Menemerus bivittatus*, Sparassidae

The spider fauna of The Gambia, West Africa is widely unknown (see distribution data in Dippenaar-Schoeman & Jocqué 1997). Indeed, more than ten years on, the African Arachnid Database (AFRAD 2008) lists only five spider species as officially recorded from the country (A. Dippenaar-Schoeman pers. comm. 2007). Although The Gambia is the smallest country on mainland Africa, it contains a wide variety of habitat types, including Bijilo Forest–a 51.3 ha, rhun-palm, *Borassus aethiopum*-dominated, coastal primary forest, which stretches for approximately 2 km along the coast, some 10 km south of the capital, Banjul.

Jumping spiders (Salticidae) are diverse in Bijilo Forest, with at least 21 different species identified to date (DP unpublished data). All Salticidae have complex eyes with exceptional spatial acuity and some of the most elaborate vision-guided predatory strategies ever documented for any animal of their size (Su et al. 2007). Most salticids are more or less generalist predators of insects, although there are some pronounced examples of jumping spiders that have specialized preferences and exhibit prey specific prey-capture behavior (Cross & Jackson 2006). Araneophagy and prey-specific predation behavior are well known in salticids (see Jackson & Pollard 1996 for a comprehensive review), but neither of the behaviors we discuss here have been previously documented. This brief report concerns the interesting feeding behavior of two widespread Afrotropical species: *Holcolaetis vellerea* Simon 1909 and *Menemerus bivittatus* (Dufour 1831) which appear to be specialist trunk-dwellers within the forest. The former species, however, is sometimes found on hanging dead palm fronds, while the latter is often found outside the forest on vertical surfaces such as walls. Similar habitat preferences have been observed in South Africa (Cumming & Wesołowska 2004). Both represent new spider species records for The Gambia, but neither is a surprising find based on its known distribution (Wanless 1985; Wesołowska 1999, 2007; Platnick 2008). However, very little is known about the biology of these two spider species (Wanless 1985; Wesołowska 1999).

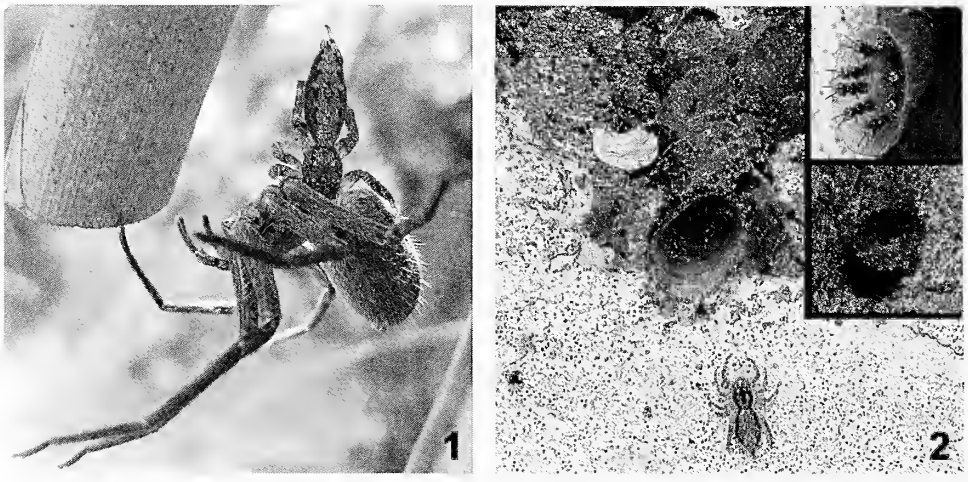
Araneophagy has been noted in the salticid literature in numerous contexts, such as targeting spiders with prey-specific tactics and singling out spiders with prey-choice behavior to name a few. The terms "araneophagy" and "araneophagic" require more refined definitions than they have at present in order to differentiate between opportunistic and specialized (not necessarily obligatory, i.e., in versatile predators) predation on spiders (R.R. Jackson pers. comm. 2008). Araneophagic behavior in *Holcolaetis* has been mentioned (without examples) by Su et al. (2007), but no published data exist and the relevant research work is still in progress (R.R. Jackson pers. comm. 2008). Here, we confirm araneophagy by recording *H. vellerea* consuming a giant huntsman spider ?*Heteropoda* sp. (Sparassidae), which is much larger than itself (Fig. 1).

Unfortunately, we did not observe *H. vellerea* capture the sparassid. One of the rear legs of the sparassid, was missing and the wound looked fresh in the field suggesting that it was lost during the attack. In addition, there was no shrinkage of the abdomen, which would have been present if the sparassid had been dead for some time. Thus, this is unlikely to be a scavenging event by *Holcolaetis*. In this instance, *H. vellerea* consumed the sparassid prey via the pedicel (Fig. 1), which serves to join the prosoma with the opisthosoma and acts as a conduit for the aorta, intestine, and the abdominal nerve (Foelix 1996). Perhaps this was also the site of the first strike. Whatever the case, the salticid must have either highly potent venom or a highly efficient attack behavior in order to overcome an equally voracious predator much larger than itself.

Portia, another araneophagic salticid certainly appears to employ attack-orientation rules, apparently as a risk-reduction strategy. These include a spider-specific decision concerning the targeted region of the prey's body (Harland & Jackson 2006). It is possible that araneophagic spiders may be able to prepare for such a specialized attack behavior after a single successful encounter with previous spider prey, although this has yet to be thoroughly investigated (Jackson & Li 2004). It has been suggested that predators that evolve prey-specific capture behavior for dangerous prey also tend to evolve specific preferences for this prey type and that, in Salticidae, their exceptionally acute vision capabilities have facilitated the evolution of such specialized behavior (Li & Jackson 1996).

In most cases, when *H. vellerea* was observed in this area, the spider was not feeding. Thus, confirmation of araneophagy as a preferred trophic strategy awaits future observations and it is currently unknown whether these are stenophagous or euryphagous predators.

Social, stingless bees (Hymenoptera, Apidae, Apinae, Meliponini) are common in the Afrotropical region, with both *Meliponula* (*Axestotrigona*) *ferruginea* (Lepeletier 1841) and *Hypotrigona gribodoi* (Magretti 1884) known to occur in The Gambia (Eardley 2004). These species usually construct their nests inside existing cavities on tree trunks with characteristic, telltale entrance tubes of wax or mud jutting out from the surface (Fig. 2). The entrance is guarded by worker bees, which form a circle around the lip on the interior of the



Figures 1,2.—Predatory behavior of Gambian salticids. 1. *Holcolaetis vellerea* feeding on a sparassid spider via the pedicel; 2. *Menemerus bivittatus* observing stingless bees *Hypotrigona gribodoi* as they enter and depart their nest (with different nest entrances inset).

tube. There is a constant coming and going of individuals entering or leaving the nest, with occasional swarming around the nest entrance. It is not uncommon to find an individual of *M. bivittatus* loitering close to, and orientated towards, the entrance watching the bees as they enter and leave (Fig. 2), but no other salticid species have been observed doing this. In a preliminary three-day survey, four out of six nests were found to have a "resident" spider present on at least two of the days. There appears to be at least two strategies by which *Menemerus* hunts these bees. In instances where the entrance tube is made of wax (probably *Hypotrigona gribodoi*), the spider is able to see the movement of the bees through the semi-transparent surface of the tube, particularly when it is viewed from below (Fig. 2). On one occasion a spider was observed leaping upwards towards the rim. It dangled there for several seconds, before losing its foothold but was unable to capture a bee. When the entrance tube is made of mud (probably *Meliponula ferruginea*) this strategy cannot be employed, because the spider cannot see the bees as they prepare to leave the nest. In this situation (and presumably also in the former), the spider probably preys on the bees as they return to the nest. It is much easier for a bee to leave the nest than it is for it to return. They seem to fly out without any trouble whatsoever, but on their return they often hesitate, hovering outside the entrance as they try to align themselves to enter. The bees are only 2–3 mm long, so even a slight breeze can send them off course. In one instance, a bee was observed to miss the entrance during its approach and it was pounced on and captured by the jumping spider.

In Azerbaijan, *Menemerus semilimbatus* (Hahn 1827) has been shown to employ a specialized, prey-specific tactic for preying on flies that differs from the standard salticid technique of orientation, pursuit and attack, as has *M. bivittatus* in India (Guseinov 2004). Indeed, the same behavior described by these authors, of the jumping spider approaching flies from behind, has also been observed in *M. bivittatus* in The Gambia (DP pers. obs.). Furthermore, *M. semilimbatus* is euryphagous and a versatile predator, using a repertoire of disparate predatory tactics, adopting different behaviors depending upon the prey type (Guseinov 2004). Our observations of this species combined with what is known about *Menemerus* species suggest that pronounced development of prey-specific tactics may be common in this genus. Our observations also indicate that *M. bivittatus* adopts prey-specific tactics for predation on stingless bees, this being something that is otherwise unknown in the Salticidae. More extensive research aimed at testing this hypothesis is planned.

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SHORT COMMUNICATION

First record of an onychophoran (Onychophora, Peripatidae) feeding on a theraphosid spider (Araneae, Theraphosidae)

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Abstract. A velvet worm (*Peripatus* sp., Peripatidae) was observed and photographed while feeding on a theraphosid spider, *Hapalopus butantan* (Pérez-Miles, 1998). The present note is the first report of an onychophoran feeding on "giant" spider.

Keywords: Prey behavior, velvet worm, spider

Onychophorans, or velvet worms, are organisms whose behavior remains poorly understood due to their cryptic lifestyle (New 1995) and by the fact they are rare in the Neotropics (Mcglynn & Kelley 1999). Consequently reports on hitherto unknown aspects of the biology and life history of onychophorans are urgently needed.

Onychophorans are almost all carnivores that prey on small invertebrates such as snails, isopods, earth worms, termites, and other small insects (Hamer et al. 1997). They are widely distributed in southern hemisphere temperate regions and in the tropics (Reinhard & Rowell 2005). Small spiders are likely to be consumed by onychophorans. Laboratory studies have focused on some aspects of the behavior of onychophorans (Read & Hughes 1987; Monge-Nájera et al. 1993; Barclay et al. 2000a,b; Sunnucks et al. 2000; Reinhard & Rowell 2005). For example, Read & Hughes (1987) observed that the onychophoran *Macroperipatus torquatus* in prey choice experiments would catch ctenid spiders instead of crickets.

Due to the cryptic lifestyle of the onychophorans, it seems unlikely that either non-cryptic or "giant" spiders represent common prey items. Here we present a chance encounter of an individual of *Peripatus* sp. (Onychophora) feeding on a large theraphosid spider, *Hapalopus butantan* (Pérez-Miles, 1998). To our knowledge, this is the first description of an interaction between onychophorans and theraphosids and also the first biological information for onychophorans in the rainforests of Brazilian Amazon.

The observations reported here were seen when we were part of an invertebrate monitoring campaign in Juruti River Plateau, Juruti, Pará, Brazil in February 2007. The area is comprised of *terra firme* (dry land) and the fieldwork that result in behavioral reports was conducted mostly in undisturbed mature forest at the Igarapé Mutum valley (02°36′10″S, 56°12′25″W) (Pinto-da-Rocha & Bonaldo 2006).

On 7 February 2007 at about 2200 h, following the collection of a nocturnal arachnid sample (active visual searching), one of us (N.F. Lo-Man-Hung) noted an onychophoran (*Peripatus* sp.) feeding on a spider (*H. butantan*) on a small leafless branch approximately 50 cm above the ground. The dorsal region of the spider was entangled by an adhesive substance probably discharged from the oral papillae of the onychophoran (Fig. 1). The onychophoran was grasping, cutting, and feeding on the ventral region of the spider's abdomen, near the spinnerets (Fig. 2). The spider was an adult female with a cephalothorax 22 mm in length, while the onychophoran had a total length of 35 mm. The onychophoran was observed to discharge further quantities of the same adhesive substance. Both the onychophoran and the spider were deposited in the collection of Museu Paraense Emílio Goeldi, Curator A.B. Bonaldo, (MPEG(ONY)0001 and MPEG(ARA)10006, respectively, under the code JURU005-181.

Unfortunately, we cannot verify whether the onychophoran actively preyed (hunted and killed) upon the spider or whether the spider was found already dead. The theraphosid *H. butantan* lives in rotten trunks or under the roots of buttress trees and are frequently found wandering on the floor forests (pers. obs.). Onychophorans are capable of preying on animals their own size, although the quantity of glue used in an attack increases up to about 80% of the total capacity for larger prey (Read & Hughes 1987). It may be that encounters with larger prey items, such as that observed by us, are more common than previously supposed.

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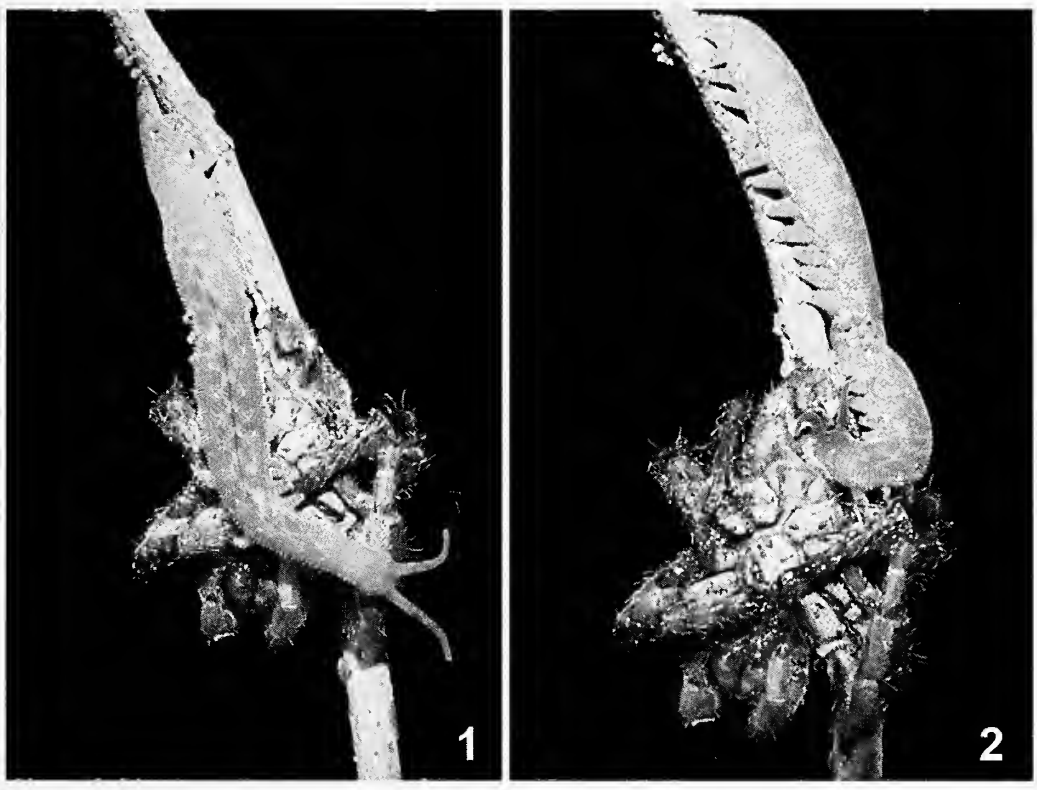

Figures 1,2.—Onychophoran (*Peripatus* sp.) feeding on a theraphosid spider (*Hapalopus butantan*) in a *terra firme* Amazonian rain forest, Juruti, Pará, Brazil. 1. Spider glued to the stick by the dorsal region; 2. Onychophoran grasping and feeding on the ventral region of the spider near the spinnerets on the abdomen (photos by F.E. Pimenta).

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SHORT COMMUNICATION

Prey and predatory behavior of two zodariid species (Araneae, Zodariidae)

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Abstract. In this study, we investigated whether two plesiomorphic zodariid species, *Lachesana insensibilis* Jocqué 1991 and *Pax islamita* (Simon 1873), both from Israel, possess adaptations for myrmecophagy similar to those of apomorphic zodariid genera. Our analysis focused on the predatory behavior and potential prey of these two spider species. We deduced that *P. islamita* does not feed on ants in nature since these were not present in its microhabitat. In the habitat of *L. insensibilis*, however, ants were very abundant, and thus they may serve as an important diet component. In the laboratory, both species were able to subdue a wide variety of prey and therefore should be considered polyphagous. They used a conditional capture strategy. Safe prey was handled by grasping and holding it in a basket-like manner. Dangerous prey such as ants were attacked, released, and finally held in the chelicerae while the spider held its own legs at a safe distance. Both species were able to overcome ants if they were not larger than the spiders. We conclude that both species possess behavioral pre-adaptations for myrmecophagy.

Keywords: Specialization, adaptations, myrmecophagy, *Pax*, *Lachesana*

With more than 800 species, zodariid spiders represent one of the most diversified families of spiders (Platnick 2008). Yet the natural history of these spiders is very poorly known. Of all 74 genera known to date, only the genus *Zodarion* has been repeatedly investigated (e.g., Harkness 1976; Pekár & Král 2001). Information on the predatory behavior and prey is available for only eight genera of zodariid spiders: *Lachesana, Lutica, Habronestes, Psammoduon, Diores, Trygetus, Zodariellum,* and *Zodarion* (Allan et al. 1996; Jocqué & Dippenaar-Schomean 1992; Marikovskij & Tystshenko 1970; Ramirez 1995; Rössl & Henschel 1999; Pekár et al. 2005). The latter four genera belong to the Zodariinae, while the first four are considered plesiomorphic. These "primitive" zodariids appear to be polyphagous, while all genera within Zodariinae are presumably myrmecophagous or termitophagous (Jocqué 1991; Dippennar-Schoeman & Jocqué 1997). *Zodarion* is apparently strictly myrmecophagous and is unable to subdue prey other than ants (Pekár 2004; Pekár & Toft, accepted).

Myrmecophagy has been observed in representatives of several different spider families beside Zodariidae, including Gnaphosidae, Salticidae, Theridiidae, and Thomisidae (e.g., Castanho & Oliveira 1997; Heller 1976; Jackson et al. 1998; Porter & Eastmond 1982). Ant-eating spiders, including *Zodarion*, use specialized prey capture behavior to overcome ants (Pekár 2004) and may possess morphological and metabolic adaptations as well (Pekár et al. 2008).

Our aim in this study was to investigate whether plesiomorphic representatives of Zodariidae feed on ants in nature and whether they possess adaptations for myrmecophagy. We examined the predatory behavior and trophic niche of two species that occur in Israel: *Lachesana insensibilis* Jocqué 1991 and *Pax islamita* (Simon 1873).

Individuals of *L. insensibilis* (body size 8–14 mm) were collected by hand in sand dunes near Mashabbim (Negev Desert, 31°0′5″N, 34°45′20″E). The burrows in the sand had no visible openings. The spiders were located by observing the search behavior of a spider-hunting wasp (*Pedinpompilus* sp., Pompilidae). Once a burrow was located by the wasp, we dug the spider out of the sand using a trowel. Altogether, 33 individuals (3 males, 6 females, and 24 juveniles) were collected. Individuals of *P. islamita* (body size 4–9 mm) were collected in a Mediterranean forest close in the Adulam Nature Reserve (Bet Guvrin, 31°38′30″N, 34°56′4″E) by sifting the leaf litter through a sieve (60 × 40 cm, mesh size 7 mm) and by hand collecting. Juvenile *P. islamita* spiders were found to hide in igloo-shaped retreats made of leaf litter particles, while sub-adult individuals rested in a crevice under stones. Altogether 59 juveniles (including sub-adults) and 2 females were collected. Identity of both species was determined using Levy (1990) and Jocqué (1991). Voucher specimens of both spider species are deposited in the collection of arachnids of the Department of Botany and Zoology, Masaryk University.

In each habitat, we investigated the potential prey of the two spider species by recording frequency of occurrence of invertebrates (> 2 mm) in the spiders' microhabitats. Our strategy for examining potential prey varied by location. In Adulam, we sifted through the leaf litter with a sieve, whereas in Mashabbim we searched the ground surface both during the day and night. All arthropods were collected and identified to order and/or family.

In the laboratory, we investigated capture success of the two spider species. Specimens of *P. islamita* were put singly in a Petri dish (diameter 6 cm). As *L. insensibilis* individuals were agitated when placed in the dish, the experiments were performed in glass containers (8 cm in diameter, 30 cm tall) filled with sand. Each spider was offered a variety of prey that either was endemic to the spider's natural environment or came from laboratory breeding cultures (Table 1). The interval between successive feedings was 10 days. Total body length of each offered prey was measured and its size was expressed as a ratio to the spider's total body length. In the case of *L. insensibilis*, nearly all prey was smaller than the spiders. Each trial with prey lasted 5 min. At the end of the trial, we assessed the prey according to whether it was attacked and consumed or untouched. The trials were recorded on video (using CANON MVX-350i camera) and the recorded predatory behavior was then analyzed.

The potential prey of *L. insensibilis* (Fig. 1) included Coleoptera imagoes (Tenebrionidae – 31%, Curculionidae – 15%, Carabidae – 5%) (altogether 51%, $n = 264$), followed by Formicidae (33%). The potential prey of *P. islamita* (Fig. 2) was comprised of Isopoda (34%, $n = 278$), Araneae (26%), and Collembola (18%). Ants were not recorded in the microhabitat.

In the laboratory, juveniles and females of *L. insensibilis* captured (i.e., attacked and consumed) various prey, mainly flies, ants and beetles (Table 1), but also crickets, spiders, termites and cockroaches. These spiders ignored true bugs and caterpillars. Males of *L.*

Table 1.—Percentage (*n*) of successful capture (i.e., attack followed by consumption) of various prey taxa in the laboratory by two zodariid species.

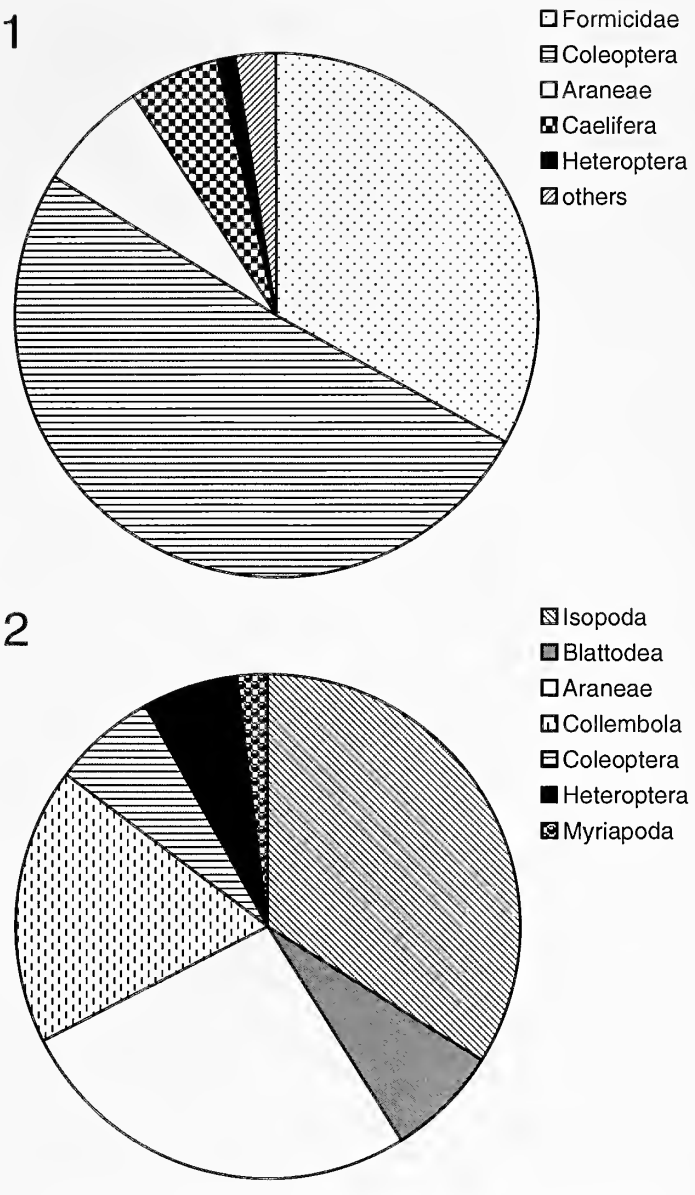
Prey type	Prey size [mm]	Zodariid species	
		Lachesana insensibilis	*Pax islamita*
Araneae (*Harpactea* sp.)	5–8	44 (19)	43 (21)
Isopoda	6–10	–	0 (10)
Collembola	2–3	–	50 (10)
Zygentoma	8–12	–	90 (10)
Blattodea	5–9	48 (21)	63 (16)
Isoptera	7–9	64 (22)	87 (30)
Ensifera (*Acheta domestica*)	6–9	65 (23)	57 (21)
Heteroptera	8–10	0 (15)	–
Coleoptera larvae (*Tenebrio molitor*)	20–25	100 (10)	70 (15)
Coleoptera imagoes (*T. molitor*)	13–15	80 (10)	–
Diptera (*Drosophila hydei*)	3–4	100 (21)	71 (14)
Lepidoptera (caterpillars)	15–20	0 (15)	–
Formicidae (*Messor* sp.)	7–12	85 (20)	53 (17)

insensibilis refused to attack any prey after molting to adult stage. It is well known that males of many spider species cease prey capture after reaching adulthood (e.g., Givens 1978). Adult males of *L. insensibilis* possess uniquely curved fangs (Levy 1990) that might handicap them in prey capture. Individuals of *P. islamita* captured mainly Isoptera, Coleoptera (larvae), Diptera, and Blattodea. They attacked woodlice but did not consume them. Ants were subdued only if they were small (less than the spider's body length).

Lachesana insensibilis individuals attacked prey either from inside the silk-lined burrow or on the sand surface within close proximity of the covered entrance. The prey was subsequently pulled inside. The burrow was narrow and long (up to 25 cm), with the top plugged with a collar made of sand. The remnants of the prey were stored in the bottom of the burrow.

Both spider species exhibited similar capture behavior that differed according to the size and safety of the prey. Springtails, cockroaches, crickets, flies, isopods, bristletails, and true bugs were grabbed by the forelegs and held in a basket-like manner using the first three pairs of legs. The bite was usually administered to the dorsal side of the thorax or abdomen and the prey, such as a cockroach, was held until completely immobilized (Fig. 3). *Tenebrio* larvae were grabbed by the forelegs and bitten on the head or at the distal end of body. Typically, the spider tried to hold on to the larvae, but if the larva struggled extensively, the spider released it (Fig. 4). Once immobilized, the larva was grabbed by its head and held in a basket-like manner. Ants, spiders, and termites were grasped and bitten on the dorsal side of the head/prosoma, and then released. After several minutes, the still-trembling prey, such as a termite, was grabbed and bitten firmly on the dorsal side of the thorax such that the termite head (and mandibles) was oriented away from the spider. The prey was never held in a basket-like manner. Based on these results, certain prey (springtails, beetles, cockroaches, crickets, flies, isopods, bristletails, true bugs) were classified as "safe" while others were classified as "dangerous" (ants, spiders, termites). *Pax islamita* was significantly more successful in capturing safe prey than dangerous prey (logistic regression, GLM – binomial errors, $\chi^2_1 = 11$, $P = 0.001$). The spiders had a 50% chance of capturing safe prey 3 times larger than their body, while for dangerous prey it was only 1.5 times larger (Fig. 5).

Results of this study show that neither *L. insensibilis* nor *P. islamita* is an ant-eating stenophagous predator. In fact, laboratory experiments suggest that both species are polyphagous. Combining the results of potential prey with data on capture success, we deduced that *P. islamita* feeds naturally on cockroaches, insect larvae, and other spiders and probably does not feed on ants at all. *Lachesana*



Figures 1, 2.—Proportion of potential prey found in microhabitats of the two study species. 1. *Lachesana insensibilis* ($n = 264$). 2. *Pax islamita* ($n = 278$).

insensibilis, however, appears to feed on ants and beetles in the field. Due to its larger body size, *L. insensibilis* has better chances of subduing ants than *P. islamita*.

Our results are in agreement with observations of *Lachesana tarabaevi* Zonstein & Ovtchinnikov 1999 from Central Asia. Individuals of this species live in similar narrow burrows and emerge at twilight to hunt at night on the surface within close proximity of their burrows. Analysis of prey remains showed that this species preys mainly on harvester ants (*Messor* sp.) and on woodlice (Zonstein & Ovtchinnikov 1999). Although we have not seen *L. insensibilis* hunt on the surface either during the day or at night, we assume it is nocturnal. We doubt that *L. insensibilis* would feed on woodlice as these do not occur on sand, but *Messor* ants were common in the habitat.

American species of the genus *Lutica* that are very closely related to *Lachesana* show similar predatory behavior. They are also fossorial, building silk-lined tunnels in sand just below the surface in the coastal sand dunes. They catch prey either from inside the burrow by hanging on the ceiling upside down and lunging through the wall or on the surface (Gertsch 1979). In the laboratory, they accepted fruit flies,

Figures 3, 4.—*Pax islamita*. 4. Handling a safe and small prey (cockroach). 5. Handling a safe but large prey (*Tenebrio* larva). Photos: S. Henriques.

houseflies, and beetle larvae but in the field they were found to feed primarily on wireworm larvae, the most abundant insects on dunes (Ramirez 1995).

Another plesiomorphic species, *Psammoduon deserticola* (Simon 1910), from the Namib Desert, attacked tenebrionid larvae on the sand's surface. In the laboratory, this spider preferred to catch tenebrionid larvae over fly larvae and Thysanura. It may feed on ants and termites as well (Rössl & Henschel 1999).

Lachesana insensibilis and *P. islamita* showed conditional capture strategy. The capture behavior of safe prey was similar to that observed in lycosids that constrain struggling prey with stout legs (Rovner 1980). Both zodariid species also possess stout legs and used them to hold all other prey in a basket-like manner. Dangerous prey, namely ants, were in turn captured using a bite-and-release tactic, similar to that of ant-eating spiders. Both *L. insensibilis* and *P. islamita* grabbed hold of an incompletely immobilized ant so the capture success depended on the relative size of the prey. Ant-eating *Zodarion* spiders deliver a bite usually to the ant's leg and wait until the ant is completely immobilized; thus, these spiders are able to overcome ants much larger than themselves (Pekár 2004). Neither *L. insensibilis* nor *P. islamita* seem to possess any morphological adaptations for myrmecophagy. It remains to be investigated whether

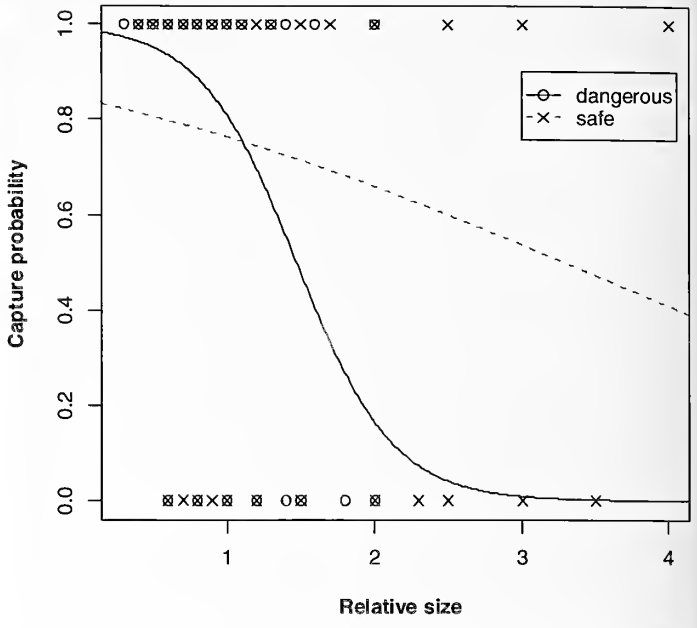


Figure 5.—Probability models for capture of dangerous and safe prey by *P. islamita*. Relative size represents the ratio of the prey body length to the spider body length.

L. insensibilis and *P. islamita* are metabolically adapted to consuming ants. *Zodarion*, for example, is adapted to such an extent that alternative prey (e.g., flies) do not provide them with the required nutrition (Pekár & Toft, accepted).

We conclude that unlike many dysderid, clubionid, lycosid, gnaphosid, salticid, or corinnid spiders that avoid ants (Bristowe 1939), "primitive" zodariid spiders possess behavioral pre-adaptations that enable them to handle ants. Yet these adaptations allow them to catch only small ants.

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SHORT COMMUNICATION

Retreats of orb web spiders (Araneae, Araneidae) as hibernation sites for terrestrial arthropods

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Abstract. Retreats of orb weaving spiders (Araneidae) were collected during the winter of 2004/2005 in northwestern Germany in order to determine the importance of these animal-made structures as hibernation sites for terrestrial arthropods. Retreats were clipped out of the vegetation, stored, and searched in the laboratory for their inhabitants. Overall, there was a high occupation of retreats by spiders, whereas only a few other arthropods were recorded. For Central Europe, there is no evidence that retreats made by orb weavers support the hibernation of a large spectrum of arthropods other than spiders. Only for spiders that may also occur as secondary occupants, retreats play an important role as hibernation sites.

Keywords: Animal constructions, animal remains as habitat, ecosystem engineering, hibernation strategy, shelter

The existence of different types of shelters may positively influence arthropod colonization of plants (Lill & Marquis 2004). Animal-made leaf shelters are created by binding, tying, rolling, or webbing leaves together with silk. Besides other arthropods like caterpillars, sawflies, ants, and beetles, various spider families construct shelters on plants (Wagner & Raffa 1993; Berenbaum 1999; Anderson & McShea 2001; Fukui 2001). Such spider retreats vary in terms of size, structural complexity, and location. The function of these constructions also varies among different spider families. For example, Clubionidae and Salticidae predominantly use woven shelters as hiding sites during day or night and for construction of egg sacs within these shelters, whereas most Agelenidae and Araneidae seek shelter while they are waiting for prey. Secondary use of such animal-made shelters by a variety of arthropods that use them as feeding sites or refuges has been observed (Carroll & Kearby 1978; Cappuccino 1993; Cappuccino & Martin 1994; Martinsen et al. 2000; Lill & Marquis 2003). From an ecological viewpoint, arthropods building such shelters act as physical ecosystem engineers: organisms that influence the resource availability for other organisms by modifying the abiotic or biotic environment (Jones et al. 1994, 1997). So far, only a few studies explicitly focus on the colonization of animal-made shelters, including spider retreats, by secondary occupants (Auten 1925; Jackson & Griswold 1979; Austin 1993; Cappuccino 1993; Lill & Marquis 2004).

We have been interested in orb web spiders as ecosystem engineers and the effects of their constructions on other terrestrial arthropods throughout Central Europe. Many orb web spiders build silken retreats where they sit and wait for prey and where they protect themselves from extreme weather conditions and from predators (e.g., Jackson & Griswold 1979; Austin 1993). We predicted that these shelters that remain in the vegetation, especially during winter, might play an important role as hibernation sites for arthropods of higher strata. Thus, a high abundance and a large species diversity of secondary retreat colonizers were expected to occur in these constructions. As far as we know, the importance of such spider-made structures for the hibernation of arthropods has not been investigated in any previous study. Other animal-made structures are also seldom considered as hibernation sites for spiders (e.g., bird nests and snail shells) (Otzen & Schaefer 1980; Klüppel et al. 1984; Bauchhenss 1995).

The study was conducted in the vicinity of Oldenburg (NW Germany). Retreats were collected haphazardly and irrespectively of plant species by sight in nine rural grasslands during two winter months (February and March) of 2005 (mean temperature: 1.2° C (Feb.), 4.0° C (Mar.)). All retreats were clipped out of the vegetation in the field and individually stored in Petri dishes. In the laboratory, all retreats were searched, and the abundance and taxa of all arthropod inhabitants recorded. Only arthropods within the retreat were collected, not those partially or completely outside. Furthermore, all retreats were stored for at least 14 days after harvesting and controlled every 2–3 days in the laboratory in order to record hatchlings or well hidden individuals. Specimens were preserved in glass tubes containing 70% ethanol. They were stored at the University of Oldenburg, Terrestrial Ecology Working Group. Retreats were primarily constructed of spider silk and small fragments of plants. Parts of prey (insect remains) were often included as secondary elements in the retreats. The retreats themselves were normally attached to infructescences of grasses or canes or to ramifications of herbaceous plants.

For the investigation of the community of hibernating arthropods in retreats of orb weaving spiders, a total of 1,004 retreats were examined (Table 1). Of these, 429 retreats (42.7%) were not colonized by any arthropods. The 575 colonized retreats yielded 605 individuals of spiders and only 15 individual insects. Thus on average, 0.6 arthropods were found per retreat. Insects were found predominantly alone in the retreats. However, four retreats were occupied by insects and spiders together. Furthermore, several retreats were inhabited by more than one individual spider.

Araneids (76.8%) clearly dominated the spectrum of inhabitants in the retreats. Theridiids (7.4%) and clubionids (5.8%) were less common. Other spider families (Linyphiidae, Philodromidae, Dictynidae, Tetragnathidae, and Thomisidae) were scarce (altogether 7.1%). In total, 412 (66.5%) of the araneids were *Larinioides* sp. (mostly juveniles and subadults; presumably all *L. cornutus* (Clerck 1757)).

Among the remaining terrestrial arthropods (3%), Coleoptera (6 species) were the most abundant secondary users (8 ind.; 1.3%). Heteroptera (3 ind.), Hymenoptera-Parasitica (2 ind.) as well as Diptera (1 ind.) and larvae of Lepidoptera (1 ind.) were extremely rare colonizers of the retreats.

Overall, our results for the Central European region implicitly show that retreats of orb web spiders in higher vegetation do not support a distinct increase of the abundance and species diversity of terrestrial insects during winter. Retreats of araneids in higher strata do not play a significant role for hibernation of arthropods other than spiders. Consultation of relevant ecological literature reveals, for example, for

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Table 1.—Identification of arthropods that had colonized 575 out of 1004 retreats of orb web spider collected during two winter months (February and March) of 2005.

Taxon	Total
ARANEIDA	605
Araneidae	476
Araneidae indet.	22
Agelenatea sp.	42
Larinioides (total)	412
Larinioides cornutus adults	132
Larinioides juveniles + subadults	280
Theridiidae (juveniles)	49
Paidiscura pallens (Blackwall 1834)	1
Theridiidae (juveniles)	48
Clubionidae	36
Clubiona stagnatilis Kulczyn'ski 1897 adults	4
Clubionidae (juveniles + subadults)	32
Linyphiidae indet.	21
Philodromidae indet.	8
Dictynidae indet.	7
Tetragnathidae indet.	6
Tetragnathidae	1
Metellina mengei (Blackwall 1870)	1
Thomisidae indet.	1
INSECTA	15
Coleoptera	8
Apionidae	
(*Perapion curtirostre*)	1
Coccinellidae	
(*Adalia bipunctata*)	1
(*Aphidecta obliteratata*)	1
(*Coccidula rufa*)	2
Carabidae	
(*Pterostichus diligens*)	2
Chrysomelidae	
(*Prasocuris marginella*)	1
Diptera	1
Nematocera	1
Heteroptera	3
Hymenoptera	2
Chalcidoidea	2
Lepidoptera	
(caterpillars)	1
ARTHROPODS (total)	620

the recorded Coleoptera, that all 6 species are eurytopic and showed no feeding preferences for spiders or insect remains. Insect remains that were included as secondary structures in some of the retreats don't seem to be an important food resource for scavengers. In conclusion, all recorded insects ean be regarded as opportunistic refuge seekers (Jackson & Griswold 1979). Thus, the importance of orb web spiders as physical ecosystem engineers in the construction of retreats is low for other hibernating terrestrial arthropods.

The function of the retreats as shelter during winter is restricted predominantly to spiders, which occur in more than half of our collected retreats. They seem to find hospitable microclimatic conditions in the retreats. Furthermore, they may be protected from natural enemies like birds (*Parus* sp. and others; Gunnarsson 2007).

Spiders hibernating in retreats may have constructed these shelters themselves or they may be secondary users. During our study, the retreats used as shelters by all of the recorded theridiids (48 ind.) had been classified by us as primary constructions of araneids. Furthermore, although most of the individuals of *Larinioides* sp. collected by us seemed to hibernate in retreats of their own species and other structures have already been shown to be important hibernating sites for this species (Kirchner 1965), several individuals were found during our study in retreats that showed typical attributes of a retreat primarily constructed by an *Araneus* species (e.g., form, color of silk). Thus, secondary use of retreats as hibernation sites seems to be quite common among spiders. In addition, it can be assumed, that some species of theridiids, actively sought pre-existing shelters of other species. They adopt the retreats of other species as a refuge or substitute for constructing their own nests (Jackson & Griswold 1979; Austin 1993).

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Figures 1–4. *A-us x-us*, male from Timbuktu. 1, Left leg; 2, Right chelicera; 3, Dorsal aspect of genitalia; 4, Ventral aspect of abdomen. Scale = 1.0 mm.

The following alternate Figure numbering is also acceptable:

Figures 1a–e. *A-us x-us*, male from Timbuktu. a. Left leg; b. Right chelicerae; c. Dorsal aspect of genitalia; d. Ventral aspect of abdomen. Scale = 1.0 mm.

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